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THE PROJECTION OF THE MEDIAL GENICULATE BODY TO THE CEREBRAL CORTEX IN THE MACAQUE MONKEY[1]

By A. EARL WALKER, M.D.

Recent studies of action potentials (Stevens *et al.* (29)) in the auditory nerve have focused attention upon the theories and neural mechanism of audition. These studies have tended to confirm Helmholtz's theory that the fibres of the basilar membrane resonate to different frequencies. The anatomical basis for the conduction from this membrane to the medial geniculate body has been determined by Held (8), Monakow (19, 20), Lorente de Nó (14), Lewy (12), Poliak (26), Winkler (32, 33), Yoshida (34, 35), Lewy & Kobrak (13), Kirilzew (10) and others. The pathway from this nucleus to the cerebral cortex is not quite so well known.

Several authors have studied the connexions of the central portion of the auditory pathway in the rabbit. Dantchakoff (3) examined the medial geniculate body after making an incision to interrupt its fibres to the cerebral cortex. Some undegenerated cells were found present in the nucleus; these were considered intercalated cells. Yoshida (34, 35) studied the retrograde cell changes after lesions in the temporal cortex of two rabbits. He concluded that the cells projecting to the cerebral cortex were mainly located in the ventral nucleus, and a few in the medio-ventral part of the dorsal nucleus. Posthumus Meyjes (17) studied both the corticopetal and corticofugal connexions in the rabbit. He found degeneration in the homolateral geniculate body, mainly affecting the dorsal parts (his nuclei *a* and *b*, and nucleus profond) after a lesion of the temporal cortex. The marginal nucleus (ventral) and the nucleus supragenicularis were never degenerated. He found also an extensive corticofugal system from almost all of the temporal area, ending mainly in the nucleus profond, and to a lesser extent in the nuclei *a* and *b*. Ohnishi (23) working on the same animal described a projection from the superior and middle temporal gyrus to the ipsilateral geniculate body.

Mettler (15, 16) investigated the corticofugal system to the medial geniculate body in the cat and monkey. He found an extensive projection system from the temporal cortex. Poliak (26, 27) has made a careful detailed study of the auditory system in the cat and monkey. He states that the fibres from the medial geniculate body project to the superior surface of the first temporal convolution, and that "Neither the ventral wall of that convolution nor any other portion of the temporal cortex (middle, inferior, temporal convolution)

[1] From the Department of Surgery, University of Iowa, Iowa City, Iowa and the Department of Neurology and Neurosurgery, University of Chicago, Chicago, Ill.

receives fibres of the auditory radiation or any other afferent fibres from the subcortical nuclei."

Nagino (22) from a study of cases of softening of the temporal lobe in man concluded that the transverse temporal convolution was related to the dorsomedial part of the homolateral geniculate body while the remainder of the first temporal convolution was in relation with the ventral part. He believed that the second and third temporal convolutions also received fibres from the geniculate body.

Many clinical cases have been reported. The majority (Berger (2), Shaw (28), Ferguson (4), Mills (18)) are concerned with reports of cases with bilateral temporal lobe lesions producing deafness. P. & R. A. Pfeifer (24) in a critical digest of the previous work show that the anterior transverse temporal convolution is the predominant receptor of the auditory projection. They clearly illustrate the course of the fibres from the medial geniculate body. A few authors have analysed cases with lesions of the temporal lobe and correlated the clinical and pathological aspects. From such a study a localization within the cortical auditory area is evident. Pfeifer (25), Kleist (11) and Fuse (7) all agree that high tones are referred to the medial portion of the transverse temporal convolution (i.e. the root of the gyrus), and low tones are mediated anteriorly and laterally in the same convolution.

The present work was undertaken to determine the extent of the entire cortical projection of the auditory pathway and to show, if possible, a spatial relation between the medial geniculate body and the cortex. The macaque monkey, the most accessible of the primates, was chosen as the experimental animal. The retrograde cell degeneration method of Nissl was selected because it was possible by this means to localize accurately the cells projecting to any portion of the cerebral cortex.

TECHNIQUE

General surgical anaesthesia was used for all the operative work. Following the operation the animals were allowed to live from 6 weeks to 3 months. The length of time within the above limits seemed to make little difference in the clearness and degree of retrograde cell degeneration. The animals were sacrificed and the vascular system perfused with saline followed by 95 per cent alcohol. After fixation in 95 per cent alcohol for a few days, the hemispheres were examined, and drawn with the aid of a camera lucida at a magnification of 1·5 and the gross lesions marked upon the drawings and described. The parts were then further fixed in 95 per cent alcohol, alcohol and ether, and embedded in celloidin. Coronal serial sections were made of both the cortex and thalamus. Depending upon the case, every section or every second or third, or in some cases every tenth, section was stained by Nissl's method. Drawings were made from the sections with the help of a Leitz enlarger and the lesions or degenerations marked in black upon the sketches.

DESCRIPTION OF THE NORMAL GENICULATE BODY

Before the experimental data are presented a note on the normal structure of the medial geniculate body (21) and its relations in the macaque monkey is pertinent. This nucleus has been previously described by Friedemann (6), Vogt (30) and Aronson & Papez (1). Although their terminology differs, the general topography of the medial geniculate body is agreed upon by all three authors. The nucleus is an elongated mass of cells lying between the lateral geniculate body and the pes pedunculi. On the basis of its cyto-architectural structure it may be divided into two parts, a dorso-medial—large-celled—and a ventro-lateral portion. The dorso-medial part is also more orally situated. The ventro-lateral portion is composed of fairly well stained and compactly arranged medium-sized cells with small processes. The dorso-medial portion is composed of larger cells, rather darkly staining and fairly compactly arranged, interspersed with a few medium-sized ones.

Lateral to the nucleus is the inferior nucleus of the pulvinar, and the lateral geniculate body, medially the nucleus peripeduncularis and anterior tegmental nucleus, and superiorly the nucleus suprageniculatus and ventral nucleus of the thalamus. A fibre lamina separates the medial geniculate body and the inferior nucleus of the pulvinar. Medial to the geniculate body the angular, small, darkly staining cells of the nucleus peripeduncularis, and the small cells of the nucleus tegmentalis anterior are readily recognized. Dorso-medial to it the nucleus suprageniculatus contains large, darkly staining, scattered cells and thus is usually easily distinguished from the large-celled portion of the medial geniculate body, the cells of which are more compactly arranged. The nucleus parageniculatus situated anterior to the nucleus suprageniculatus lies between the nucleus limitans and the medial geniculate body. It contains large, intensely stained cells, not unlike those in the ventral nucleus of the thalamus, from which it is usually separated by an acellular area.

EXPERIMENTAL DATA

Before examining the details of the auditory projection it is essential to determine the sum total of the cells of the medial geniculate body sending fibres to the cerebral cortex. For this information a knowledge of the retrograde cell degeneration in this nucleus following a hemi-decortication is necessary. In previous studies (31) it has been shown that the entire medial geniculate body, including the magnocellular nucleus, degenerates in consequence of the removal of the cortex of one hemisphere. The adjacent nuclei, suprageniculatus, parageniculatus, limitans and tegmentalis anterior are intact. It would, therefore, follow that all cells of the medial geniculate body project to the cerebral cortex.

Case 1 (N–11 R). Immature *Macaca mulatta*. On 1 June 1933, under sodium amytal anaesthesia, a large right osteoplastic flap was reflected. The

superficial cortex of the temporal lobe was removed. The flap was replaced and the wound firmly closed. The animal had an uneventful convalescence and was sacrificed 21 July 1933.

Examination of the cerebral cortex. Grossly there was a large lesion of the tip of the right temporal lobe and the cortex about the Sylvian fissure. This involved the cortex of the first temporal convolution and the lower part of the

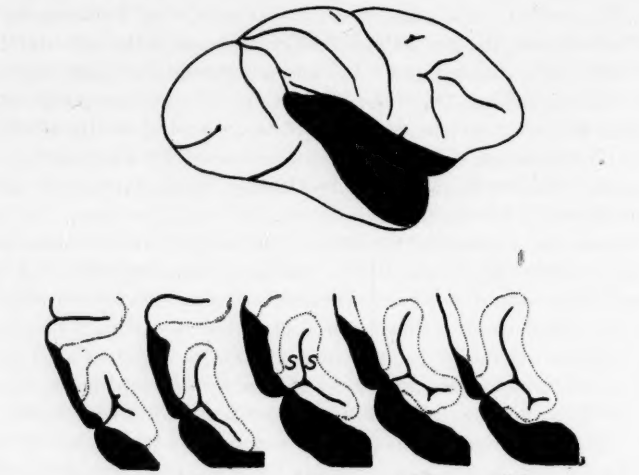

Fig. 1. The site and extent of the cortical lesion in case 1 (N–11 R). The serial sections show the amount of damage to the cortex within the Sylvian fissure. In all the illustrations, the cortical sections are from the left to the right antero-posterior.

cortex of the inferior part of the frontal lobe. A study of serial sections shows that the lesion has removed the cortex of the opercular region and the first temporal convolution and injured the anterior part of the horizontal limb of the Sylvian fissure but not the vertical limb. In the more posterior parts there is little damage to the Sylvian cortex and the cortex on the vertical limbs is not injured (Fig. 1).

Examination of the medial geniculate body. A careful examination of serial

sections of the thalamus shows that the medial geniculate body is quite free from retrograde cell degeneration.

This case clearly shows that the cortex of the lateral surface of the temporal lobe receives no, or at most an insignificant, projection from the medial geniculate body. This is quite contrary to the opinions of many previous workers. Monakow (19) and his pupils (Fuse (7)) have placed at least a part of the cortical auditory area in the superior temporal convolution. Poliak (27) states that the optimum cortical representation is in the depths of the Sylvian fissure, and that but a very few of the fibres reach the surface of the first temporal convolution. It is impossible to state from the present case that no fibres go to the superficial temporal cortex, for a considerable number of neurones must show changes before retrograde cell degeneration can be detected. The absence of retrograde cell degeneration in the thalamus following a cortical lesion may only indicate a paucity, not an absence, of thalamic projection to this area. However, as the above conclusion is based upon several cases, and agrees with findings obtained by the use of another experimental method (Poliak (27)) the result would appear to be significant.

Case 2 (E–3–35). On 8 May 1935, under sodium amytal anaesthesia, a small bone flap was turned down in the left temporal region. After reflection of the dura a small lesion was made just below the Sylvian sulcus immediately posterior to the lower end of the central fissure. The dura was replaced and tightly sutured. The animal had an uneventful convalescence and was sacrificed 28 June 1935.

Examination of the cerebral cortex. Grossly there is a lesion just below the central sulcus extending along the Sylvian fissure for a distance of 1·2 cm. It is 2–3 mm. in width and penetrates the Sylvian fissure for a distance of at least 2–3 mm. It appears to be almost entirely confined to the lower margin of the Sylvian fissure. A study of serial sections of the cortex reveals that this lesion has destroyed some cortex on the superior lip of the Sylvian fissure, and more posteriorly the cortex of the superior temporal convolution. The anterior half of the cortex of the inferior lip of the Sylvian fissure is destroyed down to the vertical limb. The posterior portion is relatively free from damage. The vertical limb of the Sylvian fissure is little damaged (Fig. 2).

Examination of the medial geniculate body. At approximately the beginning of the middle third of the medial geniculate body there is an extensive area of retrograde cell degeneration involving most of the cells in the dorso-lateral angle. More anteriorly it becomes lower in the nucleus and at about its middle involves the infero-lateral corner. Still farther anteriorly this area of degeneration becomes quite complete, involving all the cells, and reaches to the rostral extremity of the medial geniculate body. It does not involve the magnocellular portion of the nucleus (Fig. 3).

Case 3 (0–7). Immature male *Macaca mulatta.* Under ether anaesthesia 30 October 1931, a large left parietal bone flap was reflected. Three small linear incisions were made in the substance of the post-central gyrus. A punc-

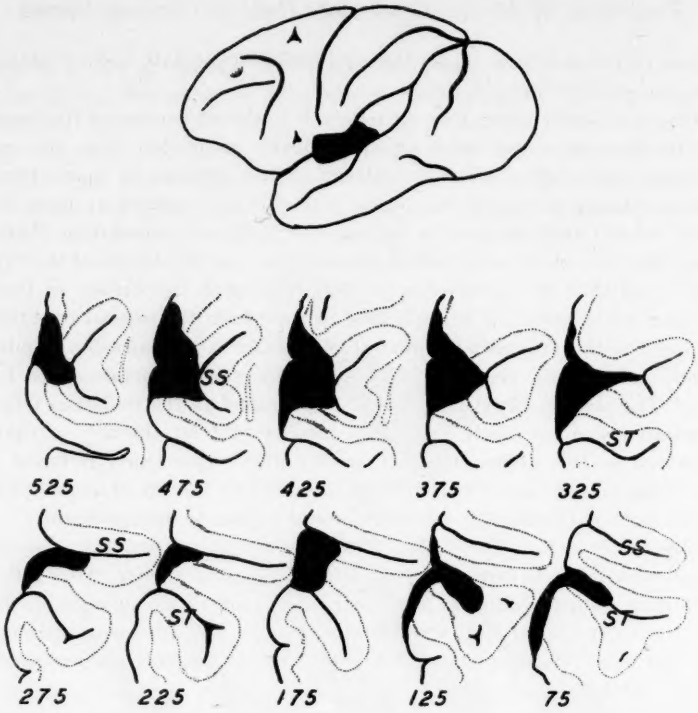

Fig. 2. The site and extent of the cortical lesion in case 2 (E–3–35).

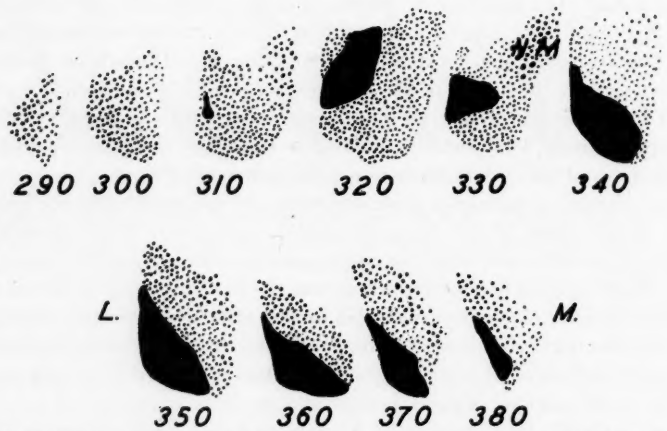

Fig. 3. To show the retrograde cell degeneration in the left medial geniculate body in case 2. The posterior sections of the geniculate body are to the left, the anterior ones to the right in the illustrations.

ture wound was made in the inferior lip of the Sylvian fissure just anterior to its junction with the superior temporal sulcus. The dura was then sutured and the flap replaced. After a rather stormy immediate post-operative course the animal recovered and was sacrificed 12 December 1931.

Examination of the cerebral cortex. Only the lesion of the Sylvian region will be described, as the others are irrelevant to the present subject. Grossly there is a small linear incision in the superior part of the first temporal convolution paralleling the Sylvian fissure just below the anterior extremity of the intraparietal sulcus. This is 1–2 mm. in length and about 1 mm. in width. It lies about 0·6 cm. from the junction of the superior temporal sulcus with the Sylvian fissure. Microscopic examination of serial sections of the cortex shows

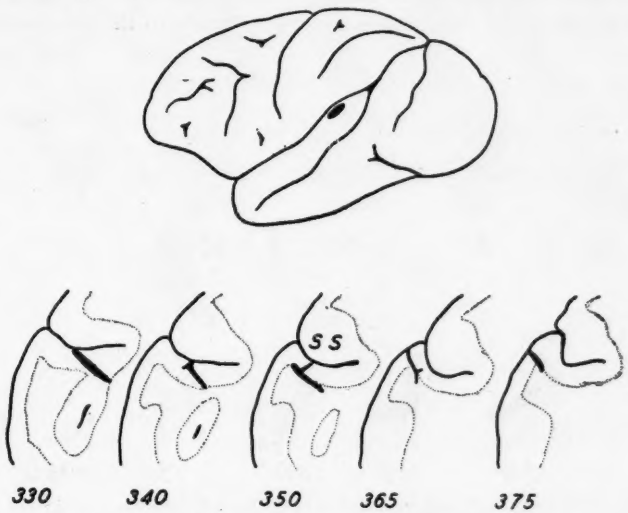

Fig. 4. The site and extent of the cortical lesion in case 3 (0–7).

that this lesion extends forward in the Sylvian fissure so that its anterior extremity damages a part of the cortex of the vertical limb of the Sylvian sulcus. The posterior portion of the incision is posterior to the vertical limb. Very little cortical substance has been actually destroyed, but the passage of the scalpel has severed a number of axones passing to the inferior lip of the Sylvian fissure (Fig. 4).

Examination of the medial geniculate body. Approximately the posterior half of the medial geniculate body is normal. About the beginning of the magnocellular portion of the nucleus there is a small area of degeneration just above the inferior angle of the medial geniculate body. This becomes larger anteriorly and extends linearly along the infero-lateral border reaching almost to the anterior extremity of the medial geniculate body although it becomes much

smaller anteriorly. The area of degeneration is well defined throughout its extent, although in many places a few normal cells are present in the degenerated areas (Fig. 5).

Case 4 (Y–5). Immature male *Macaca mulatta.* On 30 October 1935 under sodium amytal anaesthesia bilateral osteoplastic craniotomies were performed. After reflection of the dura on the left side a lesion was made in the upper margin of the superior temporal convolution just below the inferior end of the intraparietal sulcus. On the right side the cortex on either side of the Sylvian fissure was superficially undercut. The dura was firmly closed on both sides. The animal had an uneventful convalescence and was sacrificed 14 December 1935.

Examination of the cerebral cortex. Serial sections of the right cerebral hemisphere show that the lesion is entirely confined to the superficial cortex

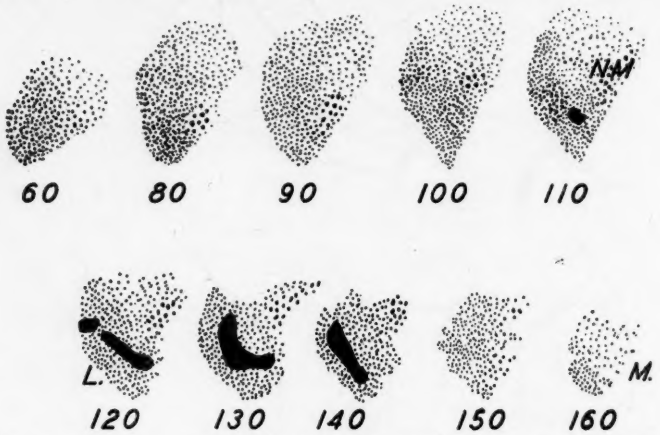

Fig. 5. The retrograde cell degeneration in the medial geniculate body in case 3.

adjacent to the Sylvian fissure. The right medial geniculate body reveals no evidence of retrograde cell degeneration, thus confirming the findings in case 1. Gross examination of the left hemisphere showed a rectangular-shaped lesion posterior to the central sulcus extending to the Sylvian fissure. Microscopic examination of serial sections of the cerebral cortex reveals that the lesion has damaged only a small part of the superior temporal convolution in its middle third. The injury does not extend to the surface of the convolution but only involves the cortex of the superior lip. The damage is almost entirely confined to the koniocortex (Fig. 6).

Examination of the left medial geniculate body. Microscopic examination of serial sections of the thalamus shows a severe retrograde cell degeneration in the left medial geniculate body. The posterior part is normal but the anterior three-fourths is largely degenerated. The degeneration is most pronounced in

the ventro-lateral portion of the nucleus and the dorsomedial portion containing the nucleus magnocellularis shows little change (Fig. 7).

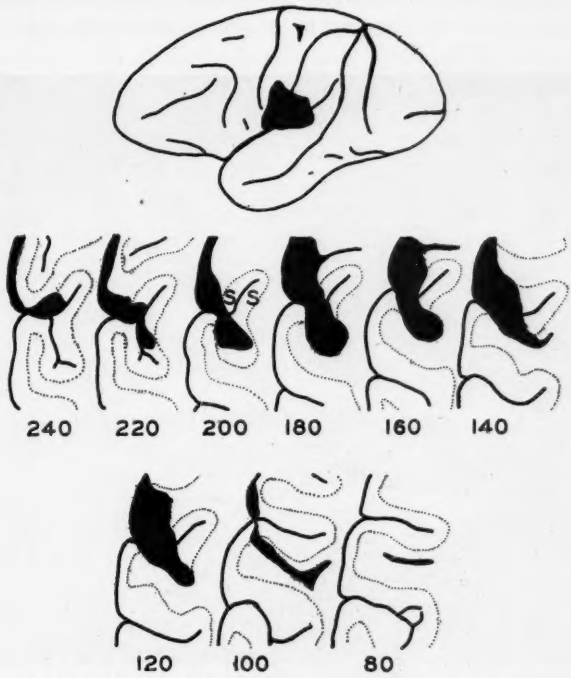

Fig. 6. The site and extent of the cortical lesion in case 4 (Y 5).

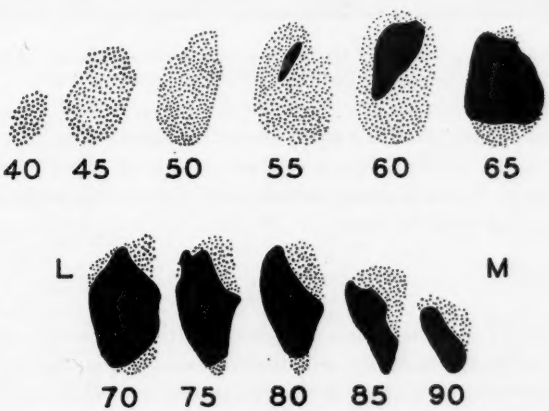

Fig. 7. To show the retrograde cell degeneration in case 4.

While the lesion is not quite so extensive as might be desired, it is localized to the koniocortex of the superior temporal convolution and has caused a complete degeneration of two-thirds of the ipsilateral medial geniculate body. The lesion extends on the superior lip of the superior temporal convolution

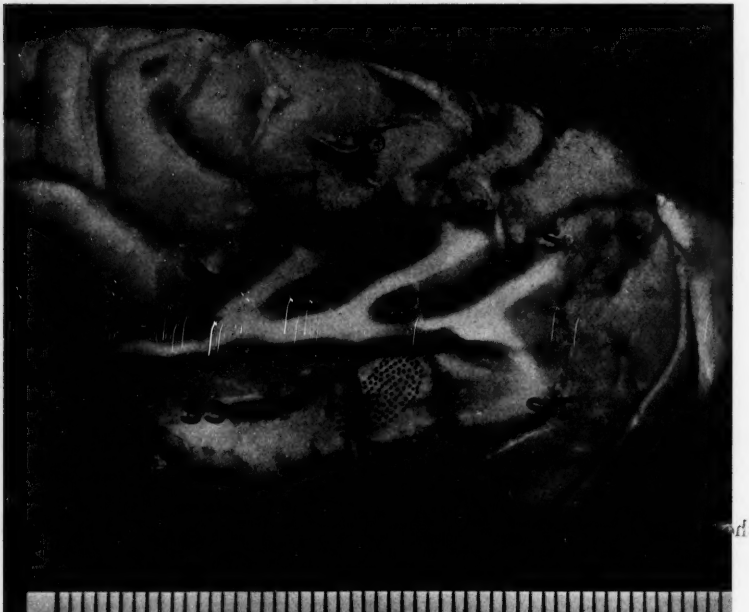

Fig. 8. The position and extent of the auditory koniocortex is indicated by the stippled area on the superior surface of the first temporal convolution.

not more than 0·5 cm., and in no place reaches the lateral surface of that convolution. This case presents strong evidence in favour of the premise that the cortical auditory region is confined to a small area on the superior surface of the first temporal convolution.

DISCUSSION

A cursory survey of these cases suggests that there is a well-localized cortical receptive area for the auditory radiation. This area would seem to be in the posterior half of the inferior lip of the Sylvian fissure. While it would be quite possible to outline the area using the retrograde cell degeneration technique

in a large series of cases, an easier method is possible. Since the somatosensory and visual primary cortical areas have typical cyto-architectural patterns (koniocortex), it would seem probable that the auditory projection area might also have a distinct cyto-architecture, with many of the characteristics of the other primary projection areas. Accordingly the cyto-architecture of the Sylvian cortex was studied not only in these cases but in a number of normal brains. It was found that along the inferior lip of the Sylvian fissure several different cyto-architectural fields are present. On the most lateral part of the lower lip of the Sylvian fissure is area 22, but more mesially this gives way to a distinct type of cortex, which has the characteristics of koniocortex. This area is located in the posterior part of the Sylvian fissure. It extends along the lower lip for only 6–8 mm. and is about 4 mm. in width. This region is situated on a small elevation to which Poliak (27) has previously called attention, and suggested that it might be a rudimentary transverse temporal gyrus (Fig. 8). As all the above lesions in which degeneration was found in the medial geniculate body damaged this area, it is very probably the cortical representation of the auditory system. Such a localized cortical auditory area would confirm the researches of Henschen (9), Flechsig (5), Pfeifer (25) and Poliak (27).

Accepting this to be the cortical auditory area, it is obvious that the projection from the medial geniculate body is not a diffuse one, but that a point to point relationship is present between the latter and the auditory koniocortex. The precise spatial relationships can only be determined by a study in which the auditory koniocortex can be exactly defined. Unfortunately such is impossible in these cases because the sections of the cerebral cortex are cut at an oblique angle to the superior surface of the first temporal convolution. However, case 3 suggests that patterns or figures may be projected from the medial geniculate body to the cerebral cortex, just as Poliak (27) has shown occurs in the visual system.

SUMMARY

From a study of the retrograde cell degeneration occurring in the medial geniculate body after lesions of the temporal cortex in the macaque monkey it is concluded:

(1) That the projection of the medial geniculate body to the cerebral cortex is confined to a small area on the superior surface of the superior temporal gyrus.

(2) That there are distinctive spatial relationships between the medial geniculate body and the cerebral cortex.

It is a pleasure to acknowledge the kindness of Dr Stephen Poliak. The present work was not only suggested by him, but he has very kindly allowed me to include in this study one of his cases (case 3). He has also given many

helpful suggestions and criticisms. I wish to thank Dr Percival Bailey for his kind advice and encouragement in this work. Valuable technical assistance has been rendered by Miss G. Ruhland and Miss K. Mahoney.

LIST OF ABBREVIATIONS

CS Sulcus centralis.
IP Sulcus precentralis inferior.
IS Sulcus intraparietalis.
L Lateral aspect of the corpus geniculatum mediale.
M Medial aspect of the corpus geniculatum mediale.
NM Corpus geniculatum mediale pars magnocellularis.
SS Sulcus sylvii.
ST Sulcus temporalis superior.

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AN EXPERIMENTAL INVESTIGATION OF THE CEREBRAL HEMISPHERES OF *LACERTA VIRIDIS*

By F. GOLDBY

Almost all our knowledge of the structure of the reptilian brain is based on the histological study of normal material. The limitations of this method are too well known to need detailed discussion. By its use it is rarely possible to trace any fibres with precision from their origin to their termination. Only comparatively large bundles of fibres can be followed accurately, and these are usually composite, difficult and sometimes impossible to disentangle into their component parts. The direction in which any given fibre normally conducts is often left in doubt. One can, in short, do little more than map in broad outline the chief cell masses and fibre tracts, an insecure foundation on which to base functional or phylogenetic conclusions.

Conclusions of this kind have been frequently drawn, however, particularly in relation to the so-called neopallial primordia at the anterior end of the hemisphere. It was decided therefore to investigate the connexions of this region by the Marchi degeneration technique. In addition various parts of the brain have been stimulated electrically, and the results of the removal of large parts and in some cases the whole of both hemispheres have been studied; these experiments have been few in number, and proportionate caution must be used in basing conclusions on them.

The work has been done in the Anatomy Department of the University of Cambridge. I am particularly indebted to the technician, Mr Walter Calcott, for the preparation of the Marchi series of sections.

MATERIAL AND METHODS

Specimens of *Lacerta viridis* with ether as an anaesthetic were used in all the experiments.

Degeneration experiments. The skull was opened with a dental drill, the dura incised and a lesion made in the brain, sometimes with a cautery, sometimes by cutting with a fine knife. The olfactory bulbs, tracts and cerebral hemispheres are all easily accessible in this way. The opening in the skull was closed with a little cotton-wool on which a melted mixture of beeswax and resin was painted. This made a firm adhesive dressing and an adequate substitute for the bone removed. The mortality was fairly heavy, due as much to the general condition of the lizard before the operation as to the operation itself. In a few cases death was due to bleeding into the cranial cavity. Warmth is essential to satisfactory recovery; a temperature of between 70 and 80° F. was maintained in the cages.

After varying periods the lizards were killed, the skulls opened, and the brains fixed *in situ* with formalin. The brain was removed from the skull the next day and treated by the Marchi technique. All were cut in serial sections, a few in celloidin but most in paraffin.

No staining of degenerated fibres was found in brains which had been obtained less than 3 weeks after the operation. Of the six specimens which gave positive results, one had lived 29 days, two 37 days, and the others 33, 34, and 35 days respectively, from the date of operation. Probably the optimum period is about 34 days.

The results were not easy to interpret. Many fibres in these brains are not myelinated, and even those that are do not produce a very plentiful crop of fat droplets when degenerated. Artefacts in the shape of a fine sprinkling of black droplets in tracts that could not possibly have been affected by the operation were frequent. All the lesions were unilateral, and Marchi staining in a tract was considered as good evidence of degeneration resulting from the operation only when a definite difference, constant through the series, could be observed between the tract in question and the same tract on the normal side. The large number of unmyelinated fibres and the difficulty of keeping the animals alive for a long enough period are serious limitations to the usefulness of the method with this species and in this climate.

Stimulation experiments. A large bone flap on the dorsum of the head was cut with a small circular saw on a dental drill and turned back. The dura was dissected away and the midbrain and forebrain exposed. Faradic stimulation was used with fine bipolar electrodes of silver wire, the animals being under fairly deep ether anaesthesia.

Ablation experiments. Apart from the smaller lesions made in the degeneration experiments, complete decerebration was attempted in three cases and a hemi-decerebration in one. A bone flap was turned back and one or both hemispheres cut away anterior to the optic chiasma. After bleeding had stopped the flap was replaced and sealed in position with beeswax and resin. These animals were not easy to keep alive, but one, after removal of most of both hemispheres, lived for 17 days. After death the brains were removed and cut in serial sections so that the amount of tissue destroyed at the operation could be determined.

DEGENERATION EXPERIMENTS

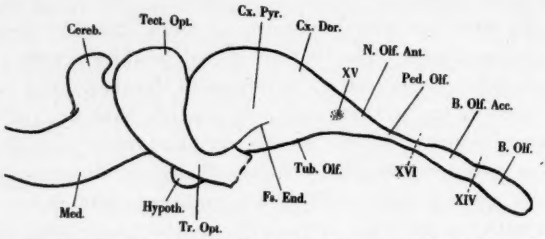
The first series of experiments was designed to investigate the primary olfactory connexions of the hemisphere.

Lizard XIV. Right olfactory bulb destroyed with the cautery; killed after 34 days; Marchi's stain.

The sections showed almost complete destruction of one olfactory bulb. The accessory bulbs, being well behind the main bulbs, were both intact. In Text-fig. 1 the mark XIV shows the posterior limit of the tissue destroyed.

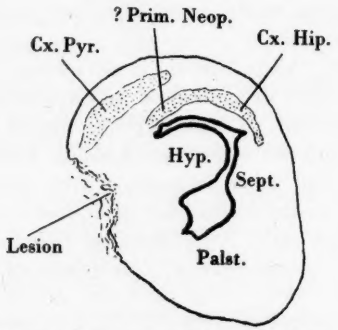
Degeneration in the olfactory tracts was slight but definite on the injured

side. Fine black stippling could be traced from the deeper parts of the injured bulb to a superficial position in the peduncle. It could not be traced further than those cells that extend from the hemisphere into the root of the peduncle —Herrick's anterior olfactory nucleus. No significant degeneration could be seen in the hemispheres posterior to this. The lateral olfactory tract, the cortex, the paraterminal body (septum) and striatum were all free from degenerated fibres. The scantiness of degeneration even in the olfactory peduncle is a surprising feature of this specimen.



Text-fig. 1. A sketch of the lateral aspect of the brain of *Lacerta viridis*. XIV and XVI mark the posterior limits of the parts destroyed in these two lizards, and XV the site of the lesion in lizard XV.

Lizard XV. A small lesion was made with the cautery in the lateral part of the root of the olfactory peduncle and the animal killed after 35 days. Marchi's stain.



Text-fig. 2. Lizard XV. Transverse section to show the position and extent of the lesion.

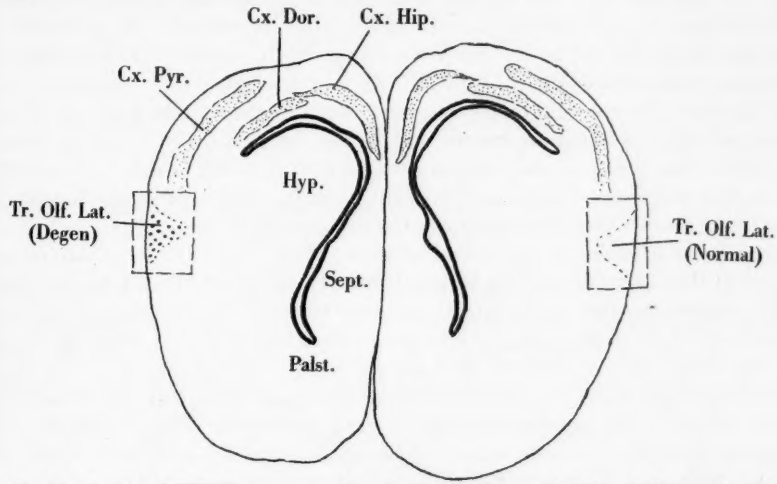
The sections showed a lesion ventro-laterally situated in the posterior part of the anterior olfactory nucleus (Text-fig. 1, XV, and Text-fig. 2). It divided the lateral olfactory tract and involved the pyriform cortex to a small extent.

Marked degeneration could be traced back in the lateral olfactory tract to the amygdaloid region of the hypopallial ridge or Hunter's eminence. It was lost in the core of a nucleus to which many names have been given: archistriatum (Kappers), nucleus occipitobasalis (Meyer), nucleus sphericus

(Edinger), etc., and which corresponds in part to the amygdaloid complex of mammals. The degeneration was more marked in the anterior than in the posterior extent of this tract.

Degeneration could also be traced ventro-medially from the lesion into the superficial aspect of the olfactory tubercle and, less certainly, into the olfacto-striatum.

A characteristic of degenerated tracts common in this series of experiments was shown by this specimen. In addition to the ordinary Marchi stain the tract showed a loose reticular structure in contrast to the finely granular appearance of the normal tract in transverse section.



Text-fig. 3. Lizard XVI. Transverse section showing the degenerated lateral olfactory tract. The rectangular outlines indicate the areas photographed in Pl. I.

Lizard XVI. The right olfactory bulb and anterior part of the peduncle were destroyed with the dental drill, and the animal killed after 37 days. Marchi's stain.

The sections showed complete destruction of the right main and accessory olfactory bulbs. In Text-fig. 1, XVI marks the posterior limit of the tissue destroyed.

Degenerated fibres could be seen peripherally in the injured peduncle and traced back to the anterior olfactory nucleus where they became scantier and disappeared completely dorso-medially. Dorso-laterally the degeneration was rather diffuse but behind this level became concentrated in the lateral olfactory tract and could be followed into the amygdaloid region. The photographs (Pl. I and Text-fig. 3) are taken from a transverse section about the middle of the hemisphere where the tract is still superficial and compact. In this specimen the black stippling was much more marked than the reticulated

appearance mentioned for lizard XV. From the point of view of the Marchi staining this is the best specimen in the series.

In the ventro-medial part of the anterior olfactory nucleus degenerated fibres were scanty, but could be traced through into the superficial aspect of the olfactory tubercle and paraterminal body (septum). No further significant evidence of degeneration was found.

The following conclusions seem justifiable on the basis of these experiments, remembering always that they apply only to myelinated fibres.

Olfactory fibres which arise in the main olfactory bulb run superficially in the peduncle and end for the most part in the anterior olfactory nucleus. Few if any of these fibres run directly to the olfactory centres in the hemisphere behind this nucleus. Fibres from the accessory bulb, on the other hand, appear to run mainly through the anterior olfactory nucleus and to constitute the main part of the lateral olfactory tract. Many of these fibres reach as far as the amygdaloid region, but some end on the way, probably in the pyriform cortex. The evidence also suggests that olfactory fibres which run directly to the septum and olfactory tubercle are of similar origin. Here one is dealing with far fewer fibres and the conclusion is less certain.

The constitution of the lateral olfactory tract of reptiles is of interest in view of Herrick's work on amphibians (1921). He has shown that in Anura there are two components of the lateral olfactory tract: (i) ventro-lateral, from the accessory bulb to the amygdaloid nuclei, and (ii) dorso-lateral, from the main bulb to the lobus pyriformis. This was the result of histological investigation, and the degree to which either of these tracts is a direct bulbar connexion and not relayed in the anterior olfactory nucleus is not clear. This subdivision is not found in the Urodela, where the accessory bulb is less distinct from the main bulb, and no clearly differentiated amygdaloid nuclei exist.

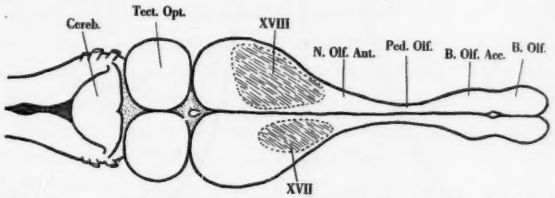
The accessory olfactory bulbs receive their afferent fibres from the vomero-nasal organs, so that in lizards it appears that the amygdaloid nuclei have developed largely under the influence of impulses that come from these organs. In this respect they resemble the Anuran amphibia. The absence of a vomero-nasal organ in the Crocodilia may account for the apparent lack of differentiation in the amygdaloid region as seen in Crosby's figures.

In mammals the condition is not yet clear. Cajal has denied any direct connexion of the lateral olfactory tract with the amygdaloid complex, and in the anosmatic dolphin this complex remains well developed. Other workers, Röthig, Herrick, Johnston and Loo in marsupials, and Herrick in the rat, have described such a connexion, but the histological evidence suggests that the lateral olfactory tract receives fibres from all parts of the main and accessory olfactory bulbs indiscriminately. There may therefore be well-marked differences between the mammals and the reptiles in the relationship of the amygdaloid complex to the vomero-nasal inflow, and this throws some doubt on the rather exact homologies between reptilian and mammalian amygdaloid

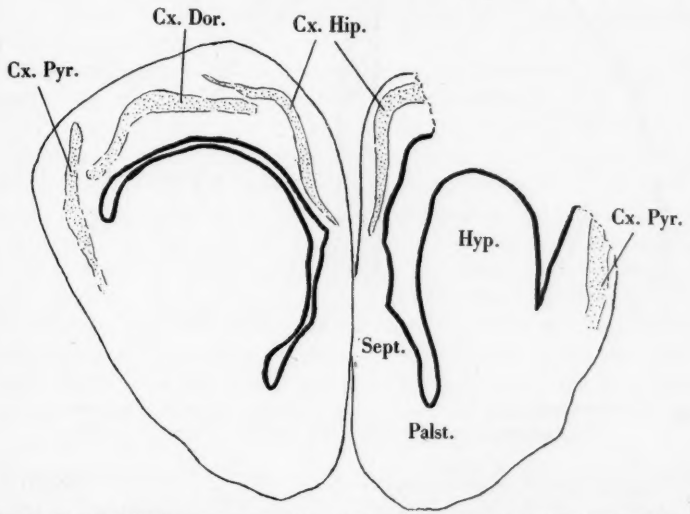
nuclei that have been instituted by Johnston (1922). In reptiles, apart from Crocodilia, it appears that vomero-nasal impulses have been an important factor in the differentiation of the amygdaloid nuclei. In mammals the evidence is against any predominant influence of this kind.

The second series of experiments bears upon the efferent connexions of the cortex and corpus striatum, and was as follows:

Lizard XVII. A longitudinal incision was made in the dorsal aspect of the hemisphere just behind the anterior olfactory nucleus. The animal was killed after 37 days and Marchi's stain was used.



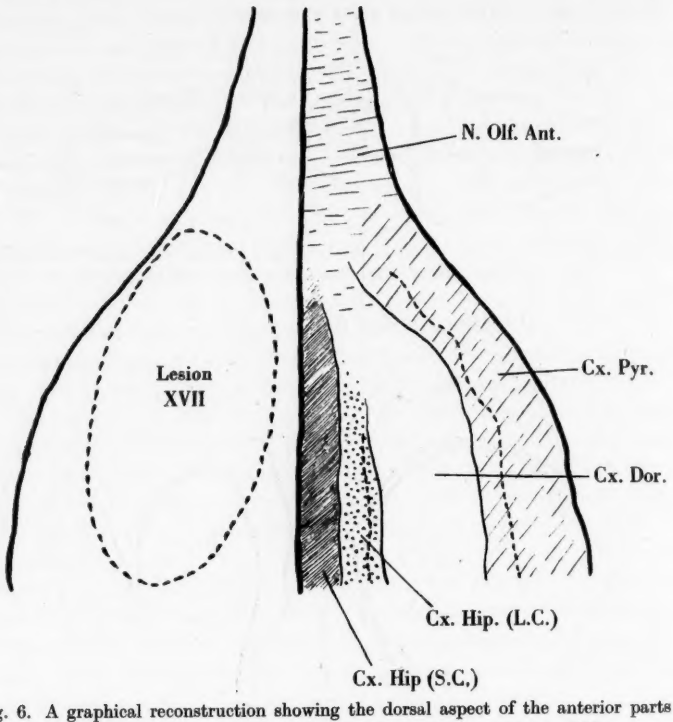
Text-fig. 4. Sketch of the dorsal aspect of the brain of *Lacerta viridis*. XVII and XVIII show the superficial extent of the lesion in these two lizards.



Text-fig. 5. Lizard XVII. Transverse section showing the extend of cortex destroyed at about the middle of the lesion. The underlying hypopallium is intact.

The sections showed almost complete destruction of the dorsal cortical area with slight damage to the anterior olfactory nucleus. The lateral part of the hippocampal and the dorso-medial part of the pyriform area were slightly involved. Text-fig. 4, XVII, shows the approximate position and extent of

the lesion. Text-fig. 5 is a transverse section through about the middle of the lesion; it shows that in spite of the extensive destruction of cortex, the hypopallium and corpus striatum generally have escaped injury. Since much has been written about the homologies of this particular region of the cortex, a graphical reconstruction has been prepared in Text-fig. 6 to show the exact areas involved. The figure gives a dorsal view of both hemispheres anterior to the lamina terminalis and the commissures, extending forwards to the root of the olfactory peduncle. Measurements were taken at right angles from the



Text-fig. 6. A graphical reconstruction showing the dorsal aspect of the anterior parts of the hemispheres of *Lacerta viridis*. For description, see text, p. 338.

medial sagittal plane to the margins of the cortical areas and plotted on the right-hand side of the figure. Only areas whose boundaries are so clear and definite as to be beyond all controversy have been marked. The intermediate dorsal area has been left unshaded and only its medial and lateral margins marked by interrupted lines. It is overlapped medially by the hippocampal and laterally by the pyriform cortical areas, De Lange's medial and lateral superposition. Anteriorly it can be seen that all the areas blend with cells scattered in the olfactory peduncle for which Herrick's name, nucleus olfac-

torius anterior, is adopted. In order not to confuse the picture the area destroyed by the lesion is marked on the opposite hemisphere.

This area covered by the lesion includes all the antero-dorsal parts of the hemisphere which can conceivably be reached by fibres of the lateral forebrain bundle system, except the anterior olfactory nucleus. Actually few if any fibres of this bundle can be traced into the region of the anterior olfactory nucleus. It is therefore true to say that the so-called primordium neopallii (Elliot-Smith), or the primordium of the general cortex (Crosby), or the parapyriform neopallial primordium (Dart), has been wholly, or in large part, destroyed by the lesion.

I feel bound to put the reasons for this conclusion at length, since I have been unable to define such a primordium in *Lacerta viridis* as a clear-cut cortical area. All that there appears to be is an ill-defined area including parts of what has been called dorsal cortex (subiculum, Dart), the pyriform area, and perhaps the nucleus olfactorius anterior, which appear to have connexions with the lateral forebrain bundle. In this species I have been unable to find anything so definite as the parapyriform and parahippocampal primordia described by Dart, nor indeed to find the thalamic radiation in the medial forebrain bundle on which so much of his interpretation rests. These findings, or lack of findings, are derived from a study of normal brains stained by the usual histological methods.

Evidence of degeneration in this specimen was extremely scanty. A fine black stippling was rather more marked in the alveus system on the injured side medial to the lesion, and could be traced, but with some uncertainty, into the dorsal part of the homolateral paraterminal body (septum). In a few of the sections behind the lesion the forebrain bundles on the injured side seemed to show similar slight evidence of degeneration, but as the appearance was not consistent from section to section, it can probably be discounted.

No other evidence of Marchi degeneration was found, but the paraterminal body on the injured side was, as a whole, smaller than on the normal side. Its cells appeared shrunken, hyaline and very refractile, but this cannot be counted as firm evidence of degeneration in the absence of any cell stain.

Lizard XVIII. A lesion was made with the knife in the antero-lateral part of the cortex. It was more extensive than in lizard XVII. The animal was killed after 33 days and stained by Marchi's method.

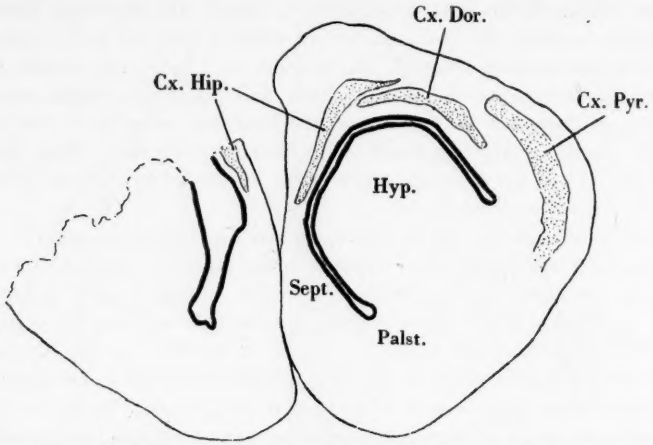
The approximate superficial extent of the lesion is shown in Text-fig. 4, XVIII. In the sections a large lesion was found in which nearly the whole of the dorsal cortex and all but the most ventral part of the pyriform and the most medial part of the hippocampal cortex had been destroyed. There was no damage posterior to the lamina terminalis. Text-fig. 7 is a transverse section through about the middle of the lesion, and it can be seen that there is also fairly extensive damage to the dorso-lateral part of the hypopallium, but that the palaeostriatum and septum are intact.

Anterior to the lesion no evidence of degeneration was found. On its medial

side rather doubtful traces were seen in the alveus system leading into the superficial part of the septum (homolateral). Similar traces were present in the anterior commissure extending into the amygdaloid region (again homolateral), but these are probably not significant.

Definite evidence of degeneration was seen in the form of a fine dust-like stippling throughout the palaeostriatum on the injured side. It could be traced back into the diencephalon in the ventral peduncle of the combined forebrain bundles, but not with certainty into the midbrain.

It was noticed in addition that the fine network of fibres in the somatic part of the palaeostriatum and the septum was looser and less uniform than on the normal side. The septum was slightly swollen as if with oedema fluid. There was no evidence of inflammation, and it seems fair to accept these changes as degenerative.



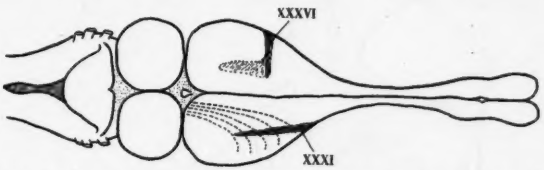
Text-fig. 7. Lizard XVIII. A transverse section showing the damage to the cortex and hypopallium at about the middle of the lesion.

Lizard XXXI. An attempt was made at hemi-decerebration, the incision being carried longitudinally between the hemispheres and then laterally behind the left hemisphere. The animal lived 31 days and was then killed and the brain stained by Marchi's method.

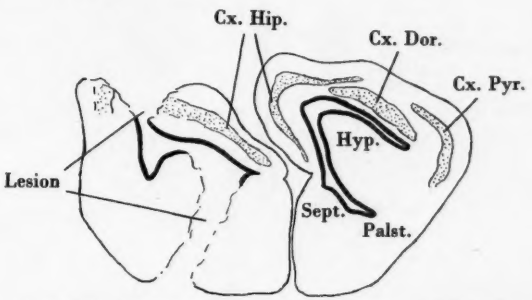
The sections showed a much less extensive lesion than had been intended. There was an incision parallel to the midline but some distance from it (see Text-fig. 8, XXXI), passing dorsally through the lateral part of the dorsal cortex and ventrally just lateral to the olfactory tubercle and the olfactory part of the palaeostriatum. Text-fig. 9 is a transverse section which shows the relation of the lesion to these parts. There was no damage posterior to the lamina terminalis, and the cerebral peduncles were both intact. There was a little damage to the lateral part of the septum. The main effect of the lesion was to divide the lateral olfactory tract anteriorly and also those fibres of the

lateral forebrain bundle which connect with the hypopallium and cortex. In Text-fig. 8 the position of these fibres has been marked with interrupted lines and their relation to the lesion can be seen.

The main positive finding in this specimen was a fairly well-marked degeneration in the ventro-medial part of the lateral forebrain bundle on the injured side. This degeneration could be traced into the subthalamic region of the diencephalon. Text-fig. 10 gives a diagram of the forebrain bundles in this part of their course. Both medial and lateral bundles are combined, and the composite tract is separating into dorsal and ventral peduncles. The dorsal



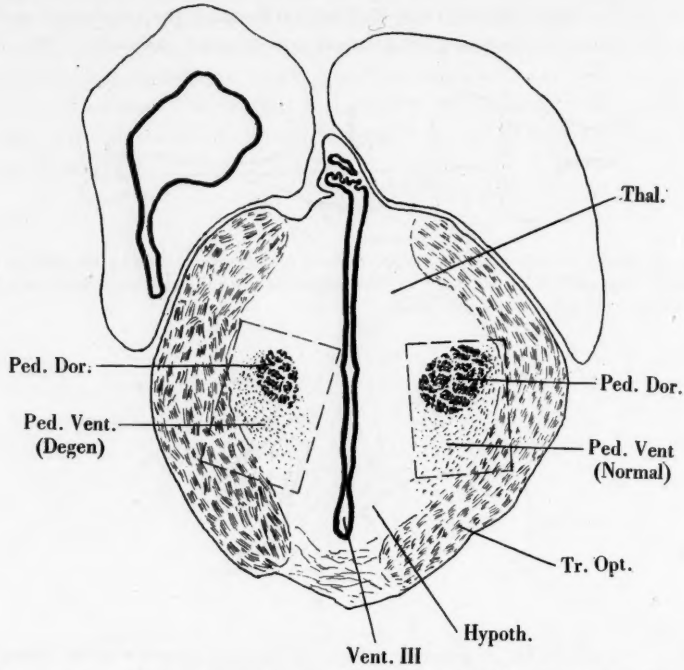
Text-fig. 8. Sketch of the dorsal aspect of the brain of *Lacerta viridis*, showing the position of the lesions in lizards XXXI and XXXVI. The dotted lines in the right hemisphere indicate the position of the lateral forebrain bundle.



Text-fig. 9. Lizard XXXI. A transverse section, considerably distorted on the injured side. The position of the cut, passing through the cortex dorsally and the striatum ventrally, is shown.

peduncle consists of coarse fibres compactly arranged (Text-fig. 10, *Ped. Dor.*). It is derived probably entirely from the lateral forebrain bundle and connects chiefly with the nucleus rotundus of the thalamus. No evidence of degeneration was found in it. The ventral peduncle, consisting of finer and more scattered fibres, is derived from both medial and lateral bundles. It runs mostly to the hypothalamus. In the photographs (Pl. II) the evidence of degeneration can be seen moderately clearly in this peduncle. There is a scattering of rather coarse fat droplets stained black in the area within the dotted line, and a fairly marked loosening of the texture of this part of the bundle, giving rather a honeycomb appearance which does not show very clearly in the photograph. These findings were consistent on the injured side throughout the diencephalon.

A little degeneration could be traced through into the midbrain, where it lay in the tegmentum, dorso-medial to the basal optic root (see Text-fig. 12, from another specimen), in the position of De Lange's tractus septo-mesencephalicus. This is shown in his Fig. 17 of *Varanus salvator*, p. 90, 1913. Most of the degenerated fibres, however, end in the diencephalon, probably in the hypothalamus.

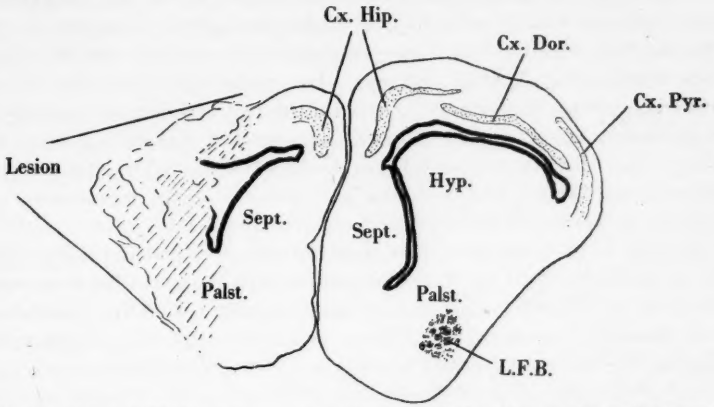


Text-fig. 10. Lizard XXXI. A transverse section about the middle of the diencephalon. The position of the forebrain bundles and their subdivision into dorsal and ventral peduncles is shown. No attempt has been made to show the degeneration in the ventral peduncle on the left side, but photographs of the areas outlined are shown in Pl. II.

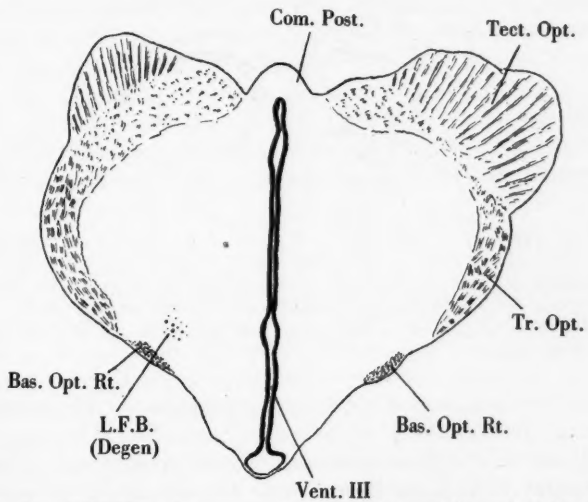
Beyond this there was considerable diffuse stippling in the hippocampal cortex and septum on the injured side, although this could not be traced posteriorly in the medial forebrain bundle. A similar finding in the stria medullaris may be significant. Some stippling among the fibres of the commissures was too diffuse to be capable of interpretation. Anterior to the lesion slight stippling and atrophy in the anterior olfactory nucleus and the olfactory peduncle was seen.

Lizard XXXVI. A transverse cut was made about half way through the hemisphere just behind the neopallial primordium. The animal was killed

after 29 days, and Marchi's stain was used. The position of the lesion is shown in Text-fig. 8.



Text-fig. 11. Lizard XXXVI. A transverse section through the lesion at the level of maximal destruction of tissue. All that part of the left hemisphere shaded obliquely is necrotic.



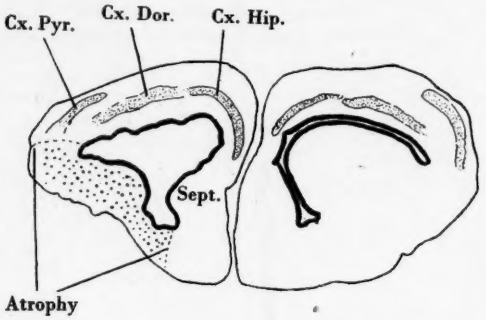
Text-fig. 12. Lizard XXXVI. A transverse section at the posterior end of the diencephalon, showing the beginning of the tectum of the midbrain. The position of the degenerated fibres is marked on the left side dorso-medial to the basal optic root.

In the sections it was found that at the level of the cut the whole striatum, with the exception of its most medial part, the pyriform cortex and the dorsal cortex had been destroyed (Text-fig. 11). Posteriorly there was some additional destruction of the dorsal cortex. The lateral forebrain bundle had been

completely divided near its anterior end, and also, of course, the lateral olfactory tract. The medial forebrain bundle was practically intact.

Posterior to the lesion degeneration was definite in the medial part of the lateral forebrain bundle and could be traced through the subthalamic region in the ventral peduncle into the tegmentum nearly as far as the level of exit of the IIIrd nerve. Text-fig. 12 shows the position of the degeneration in a transverse section at about the junction of the diencephalon and the midbrain. Comparatively few of the degenerated fibres reached this level, most of them ending in the diencephalon, probably in the hypothalamus. The lateral olfactory tract was degenerated and some fine and rather doubtful degeneration could be traced in the alveus system into the septum.

Anterior to the lesion the whole striatum was atrophied and finely stippled with fat granules (Text-fig. 13). The cortical areas and septum were normal. A little rather doubtful degeneration could be traced round the lateral angle of the ventricle into the dorsal cortical area in the region of the primordium neopallii. The anterior olfactory nucleus was not appreciably affected.



Text-fig. 13. Lizard XXXVI. A transverse section anterior to the lesion. The whole ventro-lateral sector of the left hemisphere (stippled) shows marked atrophy. Marchi staining of degenerated fibres was present in this sector, but was not nearly as conspicuous as the stippling in the figure.

These experiments suggest the following conclusions. Destruction of the dorsal cortical area anteriorly, including any neopallial primordia that may be present, leads to no definite degeneration of myelinated fibres in the lateral forebrain bundle. There is therefore no long descending tract from this region of the cortex of *Lacerta viridis* leading to centres below the forebrain, and in any way comparable with the pyramidal tracts of mammals. There was some evidence for the presence of short fibres running medially in the alveus system to the septum.

When, in addition to the destruction of cortex the striatum is also damaged, degeneration appears in the more medial and ventral part of the lateral forebrain bundle and can be traced into the diencephalon and to a small extent into the

midbrain. These fibres appear to be descending from the striatum, and comparable to some components of the ansa lenticularis of mammals.

The greater part of the lateral forebrain bundle consists of ascending fibres from the thalamus. The destination of some of these fibres is indicated in lizard XXXVI, where the anterior part of the forebrain bundle is cut off. In this anterior part degeneration is found, but can be traced only to a minor extent, and that rather doubtfully, into the lateral part of the cortex. The most anterior fibres of the lateral forebrain bundle end predominantly in the striatum itself, particularly its hypopallial part.

These results from the use of the Marchi technique, and the conclusions based on them, must be accepted with very great caution. Partly because myelinated fibres are not so numerous and partly because of the difficulty of the technique in cold blooded vertebrates, the actual histological findings are not so definite as they are in good mammalian preparations. Tracts are less clearly circumscribed and it is often difficult to be sure that a diffuse stippling is not an artefact, or that its presence on the injured side and not on the other only fortuitous.

It will be noticed that the conclusions concerning the composition of the lateral olfactory tract are really based on one specimen, lizard XIV, in which the results were for the most part negative. If in this specimen the lack of apparent degeneration in the lateral olfactory tract was due to some failure of technique, the greater part of the argument falls to the ground. In its favour it can be said that the lateral olfactory tract is one which showed evidence of degeneration more easily and more definitely than any other in this series of experiments, and that the technique used for lizard XIV was in no way different from that used for the others.

A further point that throws some doubt on the validity of these results is the lack of degeneration in some fibres which one would have expected to be affected. The alveus system was damaged, and sometimes quite extensively, in many of these experiments, yet it never showed more than very scanty evidence of degeneration. The system is known to contain many myelinated fibres, and these may of course be afferent to the cortex, but this conclusion is not secure without the corresponding positive evidence of degeneration to confirm it.

Finally, in defence of the conclusions that have been drawn, it may be said that there is some positive evidence to support all of them, and that they do not conflict with the known histology of normal material. It seems, therefore, justifiable to assume their truth provisionally and as a basis for discussion and further work.

STIMULATION EXPERIMENTS

Two of the largest specimens were used for these experiments, and with the following results.

No motor response could be obtained from any part of the hemispheres

or the olfactory peduncle with a stimulus that was adequate to evoke movements easily from the midbrain, or by direct application, from a muscle. Movements resulted from stimulation of the forebrain only after the use of a stimulus so strong that it spread even to the adjacent temporal muscle and must have affected the whole brain at least. Such movements were always mass movements of the whole body, and clearly were valueless as evidence of a specific motor function in any part of the forebrain.

Stimulation of the tectum of the midbrain led constantly to a flexion of the tail towards the side stimulated. By increasing the strength of the stimulus this movement was converted into a fairly regular side to side movement of the tail; i.e. a regular series of muscular contractions travelling alternately down the two sides of the body. The extent to which the trunk muscles were involved varied, but the whole movement was very like that of the trunk and tail in normal progression. The limbs did not take part in this movement in any co-ordinate manner. Isolated movements of the limbs sometimes resulted from midbrain stimulation, but they were weak, inconstant, and sometimes homolateral, sometimes heterolateral. They never occurred apart from tail movements.

An attempt was made to investigate the effect of simultaneous stimulation of the forebrain on movements to be obtained from the midbrain. A continuous stimulus, of a strength just sufficient to evoke movements from the midbrain, was applied to the hemisphere in the region of the dorsal cortical area. It was found that movements of the tail could still be obtained from the midbrain. They tended to be rather slower; sometimes better sustained, sometimes less in extent, but not otherwise altered in character. This effect was soon lost, and could not always be repeated after an interval for the recovery of fatigue.

Stimulation of the midbrain after the removal of the hemispheres led to the adoption of a definite posture. The forelimbs were adducted back to the trunk, with the elbow at a right angle so that the body was held just off the ground. The hindlimbs were splayed out in semi-flexion at the hip and knee. This reaction was tested in only one specimen.

ABLATION EXPERIMENTS

(i) *Partial lesions of one hemisphere*

In several lizards (e.g. lizards XVIII and XXXI) fairly extensive lesions were made in one hemisphere. Some of the hippocampal cortex, the septum and a considerable part of the striatum were intact on both sides. None of these specimens showed any defect of motor behaviour once they had recovered from the immediate effects of the operation. This was often after so short a time as one or two hours. Under the conditions of the experiments, i.e. confinement in a small cage, they did not differ to superficial examination from normal lizards. They were active and fed well. In all these specimens a con-

siderable part of the dorsal cortex including the region of the neopallial primordia had been removed.

(ii) *Hemidecerebration*

Lizard XXV. Practically the whole of one cerebral hemisphere was removed together with most of the septum and cortex of the opposite hemisphere (excluding the pyriform area). There was some slight damage to the opposite corpus striatum. The animal lived for 10 days after the operation.

This lizard remained rather sluggish. Stimuli, such as a touch or pinprick on any part of the body, led to quite normal reactions in the form of attempts to escape or run away. There seemed to be no defect in the performance of any ordinary movement, and this condition was reached within 24 hours of the operation.

It was not seen to feed at any time after the operation, but on the third day it snapped at a worm moving in its field of vision. It failed to take the worm into its mouth.

Its posture was normal, but 7 days after the operation slight hypertonus seemed to be present in the extensor muscles of the neck. At this stage, in running forwards, it made repeated leaps upwards with the forepart of its body, as if attempting to surmount imaginary obstacles. There was no further change till its death on the tenth day.

(iii) *Complete decerebration*

Lizard XXXII. It was found post-mortem that the attempt at complete decerebration in this lizard had removed all the anterodorsal parts of the hemispheres including the septum and commissural region. There was a little damage to the anterodorsal part of the thalamus. The hypopallium had been removed anteriorly, but a little of the palaeostriatum, the posterior part of the hypopallium and the amygdaloid region were intact on both sides, although much damaged by haemorrhages, the probable result of infection.

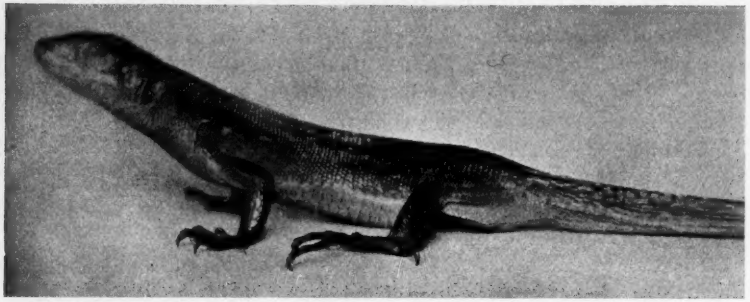
No detailed notes were kept of this lizard, but there was no obvious defect of motility or posture, and no rigidity. It was never seen to feed, and at death the intestine was completely empty. It lived 22 days.

Lizard XX. This lizard lived only 2 days. Post-mortem it was found that the whole of both hemispheres had been removed with the exception of the posterior end of Hunter's Eminence, i.e. the amygdaloid region. The preoptic nuclei, thalamus and hypothalamus were intact.

Apparently voluntary movements of the forelimbs were noted 1 hour after the operation. Four hours later the lizard could walk in a perfectly co-ordinated manner if strongly stimulated by touch or pinprick. There seemed to be a slight general increase in the tone of all the muscles of the body, most marked however in the muscles which extend the trunk and neck. It was extremely sluggish and it was difficult to determine the posture of the limbs, since they tended to remain in any position to which they were passively moved.

There was no change 24 hours later, but it was noted that it could climb up the side of its cage.

Lizard XXI. This lizard lived for 7 days. Post-mortem both hemispheres were found to be completely removed. There was in addition much diencephalic damage due to haemorrhage and infection. An abscess in the tegmentum had probably interrupted the tecto-spinal tract on one side.



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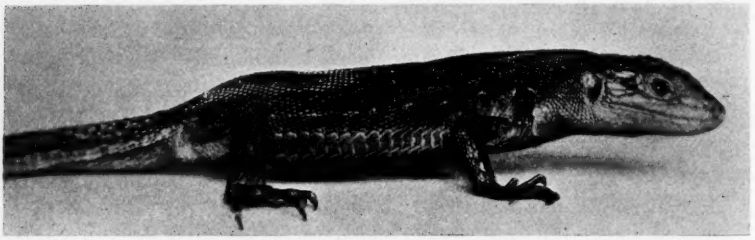

B.

Text-fig. 14. Lizard XXI. Photographs to show typical postures on, A, the second, and B, the third, day after the decerebration.

Five hours after the operation the lizard was walking normally, but showed the same sluggishness and general increase of tone as the preceding specimen. There was the same tendency to remain in any position to which it was brought by passive movement, but tilting or inversion of the whole animal always led to brisk attempts to regain a normal position.

No marked changes occurred throughout the remaining 6 days of life. As a rule it stood in an extended posture with the body lifted off the ground (Fig. 14 A), but was often found in a more normal position, although usually with the body raised above the ground (Fig. 14 B). The right eye had been slightly damaged in the operation and the head was usually held abducted towards the left.

It noticed a worm moving in its field of vision and turned towards it. On one occasion it turned and snapped when pricked with a pin, but on no occasion made any attempt to feed.

In running it held its head hyperextended and made repeated jumps into the air like lizard XXV. Its sluggishness persisted throughout the whole period of its post operative life.

Lizard XXIV. This animal lived for 17 days. After death it was found that the cortex had been destroyed in both hemispheres, except for the medial part of the hippocampal area. The septum and the greater part of the striatum were present, but much damaged by small haemorrhages. These were present also in the thalamus and hypothalamus.

In its sluggishness, a slight general increase in tone and a tendency to remain in any position in which it was placed, this lizard resembled the preceding ones. It was not seen to feed. The increase in tone was rather doubtful, and the posture was always normal, the belly not being raised off the ground except in response to stimulation. It walked quite normally and ran with no attempt to jump like lizards XXV and XXI.

DISCUSSION OF THE STIMULATION AND ABLATION EXPERIMENTS

In *Lacerta viridis* there is no region on the dorso-lateral aspect of the hemisphere or in the olfactory peduncle where faradic stimulation leads to a motor response. There is, in fact, no evidence for the existence of a pallial area with characteristics resembling those of the motor part of the neopallium of mammals. This finding is in accord with the results of Marchi experiments where no trace of a long cortico-fugal tract like the pyramidal tract of mammals could be found. The conclusions reached on p. 345 indicate that the lateral forebrain bundle consists predominantly of thalamo-striatal fibres and a strio-fugal system running to the subthalamus, hypothalamus and tegmentum. A similar fibre system is found associated with the corpus striatum of mammals, and it is with this system rather than with the internal capsule that the lateral forebrain bundle of reptiles is comparable. Although the corpus striatum and its associated fibre systems are undoubtedly related to motor function, they are not electrically excitable. Such excitability is a characteristic limited to certain parts of the neopallium of mammals, and these parts and their typical connexions do not appear to exist in reptiles.

Stimulation of the hemispheres, however, did influence movements which could be obtained from the tectum of the midbrain. The result was not obtained constantly and it needs confirmation in larger reptiles. At least it indicates that the method of simultaneous stimulation of two parts of the nervous system may lead to information about regions which give no response when stimulated alone.

As far as they concern the inexcitability of the cortex, these results agree

with those of Dr W. H. Wilson, of Cairo, who, in *Varanus* and *Uromastix*, was unable to obtain movements from the hemispheres with a stimulus strong enough to excite the midbrain. They conflict with those of Johnston (1916), Bagley & Richter (1924), and Bagley & Langworthy (1926).

Johnston obtained his results under deep chloroform anaesthesia, which he says is a necessary part of his technique. In three species of turtle and in a lizard (*Gerrhonotus*) movements were obtained from the antero-lateral part of the cortex. He does not specify the kind of movement very precisely, e.g. he states that from the antero-lateral pallial border in a turtle he obtained "movements of eyes, jaw, neck, legs and tail". These movements were not constantly homolateral or heterolateral, but only usually one or the other. He does not state how far the movements obtained in different animals resembled or differed from each other, except for two lizards. One of these, from the motor area in question, gave movements of the "foreleg, jaw and eye muscles, neck and throat muscles, and anterior body musculature". The other, from the anterior part of this motor area, gave "strong contractions of the pelvic muscles, and movements of the hindlegs", and from the lateral part of the area a "definite torsion of the forepart of the body".

Bagley & Richter and Bagley & Langworthy made use of alligators and obtained their best results without any anaesthetic. Movements were obtained from a similar motor area, and appear to have been of the same irregular type, usually involving both neck, trunk and tail and more than one limb. Single movements of a limb were never obtained. Their results differ from Johnston's in two important respects. They state that the striatum is completely inexcitable, whereas Johnston obtained movements from the striatum which he though were due to stimulation of the crus passing through it. They also state that the movements were obtained most easily from the medial side of the hemisphere (i.e. from the surface of the septum) and that the conduction of the motor impulse is down this medial wall, presumably in the medial forebrain bundle system. Johnston could get no response from the medial wall of the hemisphere in the turtle.

None of these workers found any evidence for the localization of precise movements. Johnston states "tentatively and with reserve that leg movements have been obtained most often from the anterior part of this area, and eye, jaw and neck movements from the lateral portion". Bagley & Langworthy found that the outer part of their area favoured movements of the legs, and the medio-dorsal part those of the head and tail.

It is clearly impossible to bring these varying results into any uniform scheme. It may be that different reptiles, even different species of lizards, differ far more than one would expect. On the other hand, differences in technique may also explain the inconsistences. The obvious fallacy in dealing with a small brain is the possibility of the spread of the stimulus to adjacent structures. The workers who have obtained positive results appear to have taken efficient precautions against this, and to have controlled their experiments

with care, particularly in the case of Bagley & Langworthy's experiments on the alligator. On the other hand, it is difficult to discredit negative results on technical grounds, since technical errors are more likely to give false positive results in experiments of this kind than negative ones. It is possible that the anaesthetic had depressed the excitability of the cortex although Johnston obtained his results under far deeper anaesthesia than was used here. Operative damage to the cortex and interference with its blood supply might account for negative results, but care was taken to avoid these accidents, and, as far as could be seen, with success.

In this unsatisfactory state of affairs one must be very cautious about basing any conclusions on the results of forebrain stimulation in reptiles. It can at least be said that these negative results, and Bagley & Langworthy's results, although at variance over the main question whether the cortex is excitable or not, agree in finding no evidence of a descending motor tract from the antero-lateral part of the cortex which passes like the pyramidal tract of mammals through the striatum. They indicate the possibility of the conduction of motor impulses down the medial side of the hemisphere. Histological evidence shows that such a path may be present as part of the alveus system, and the Marchi experiments suggest that it is not a long tract, but consists of short fibres which connect the cortex with the septum, whence their impulses could be relayed to lower levels in the medial forebrain bundle system.

The ease and constancy with which movements can be obtained by stimulation of the tectum of the midbrain indicate that this is a very important and perhaps the dominant motor mechanism of the lizard brain. Its extent is considerable and its histological complexity far in advance of anything found in the forebrain. It is surprising that the main response affected always the tail and trunk muscles, but this may be because in such a small animal it is impossible to localize the stimulus to discrete parts of the tectum. The larger trunk and tail movements might then overshadow the finer ones. There was some evidence that the cortex might modify the activity of the tectum, but as a whole the results suggest that the control of movements, which is a function of the motor area of the neopallium of mammals, is localized in the midbrain of reptiles. This function of the midbrain is modified in a general way, e.g. by facilitation or inhibition, by impulses from the forebrain. There is no evidence for the exact and detailed representation of movements in the hemisphere of the lizard as there is in that of mammals.

The ablation experiments are for the most part in accord with this conclusion and with the similar experiments of Steiner (1900) on the lizard, and of Bagley & Langworthy (1926) on the alligator.

It appears that large unilateral lesions of the cortex lead to no obvious change in the behaviour of a lizard. In the only case in this series (XXIV) where the cortical lesions were bilateral, the animal was sluggish, refused to eat, and showed slight hypertonus. In this animal there was some striatal

and diencephalic damage due to infection and haemorrhage. It is probable that this damage is really responsible for the changes in behaviour observed, since Steiner found that complete decortication left the animal apparently normal.

Extensive damage to the basal centres, comprising the striatum and septum or paraterminal body, led constantly to an extreme sluggishness with almost a complete lack of any spontaneous activity, an inability to feed, slight hypertonus chiefly of the muscles of the neck and trunk, and to the curious jumping gait after strong stimulation. These changes were seen even after the attempted hemidecerebration (XXV), where the whole thalamus and one corpus striatum were still intact and found to be free from any damage by infection and haemorrhage after 10 days. Steiner states that he observed the jumping gait only after the removal of the thalamus. From his diagram of the brain after the removal of the hemispheres alone it appears that a very considerable part of the striatum was left intact, and it may well be that it was the removal of this part of the striatum and not of the thalamus which led to the appearance of this type of progression in his second series of experiments. He did not check the amount of brain tissue removed after death by the method of serial sections.

Steiner observed no hypertonus and no postural change after decerebration, and with this Bagley & Langworthy are in agreement in their experiments on the alligator. As in the stimulation experiments, the negative finding is less open to criticism on technical grounds than the positive, but in spite of this it seems worth while to put these observations on lizards on record. As far as they go, they suggest on the positive side some participation of the basal centres of the hemispheres in the distribution of tone and in feeding activities. In addition these parts seem to have an influence on mechanisms in lower levels of the nervous system, perhaps of the nature of facilitation, which shows itself in the apparently spontaneous activity of the normal animal. On the negative side there is complete agreement in all the results so far published. There is no evidence from ablation experiments that any movement is localized in the forebrain in such a way that removal of the forebrain, or of any part of it, leads to the loss of that movement. In other words there is nothing to suggest a localization of motor function of the type found in the motor area of the mammalian neopallium.

Structurally there is no evidence for the presence of long efferent projection tracts from the cortex. The efferent cortical fibres are short and run mainly to the septum whence they are relayed into the medial forebrain bundle, and perhaps laterally by way of the striatum into the lateral forebrain bundle. It seems unlikely that this relay is a simple affair, transferring the impulse with little alteration to lower centres. There is some evidence that in birds the striatum is responsible for the co-ordination of different movements into an orderly behaviour sequence (the complete performance of the act of feeding is one of the simpler sequences which are dependent on the

integrity of a part of the corpus striatum in birds; Rogers, 1922), and it is likely that the basal centres of the reptilian brain have similar functions. From the results recorded above this appears to be true in relation to feeding at least. Cortical impulses will probably play upon these basal co-ordinating mechanisms, modifying their activity in some way that these experiments are too crude to reveal. They would not control movement directly, and therefore differ functionally as well as structurally from the motor parts of the neopallium of mammals.

SUMMARY

Marchi experiments

The ordinary technique was used, but it was found that a post-operative life of at least 30 days, during which degeneration could take place, was necessary. Warmth is essential during this period.

Though not so striking as the results obtained with mammalian material, positive staining of degenerated myelinated fibres was found after lesions in the olfactory tracts, the lateral forebrain bundle and, less certainly, in the alveus system.

Evidence was found for the following conclusions:

(i) Primary olfactory fibres from the main olfactory bulb are for the most part relayed in the anterior olfactory nucleus before passing to other forebrain centres.

(ii) The lateral olfactory tract consists predominantly of fibres from the accessory olfactory bulb and many of them reach the amygdaloid nuclei without an intermediate relay.

(iii) There is no efferent projection tract from the antero-dorsal region of the cortex. There is some evidence for the presence of short efferent fibres from the cortex passing medially in the alveus system to the paraterminal body (septum).

(iv) The lateral forebrain bundle contains efferent fibres from the corpus striatum, mainly its hypopallial part, which can be traced into the subthalamic region. Many end here, probably connecting with the hypothalamus. A few can be followed through into the tegmentum of the midbrain.

These conclusions naturally take no account of unmyelinated fibres.

Stimulation and ablation experiments

Under ether anaesthesia faradic stimulation of the cortex failed to elicit any motor response. From the tectum movements chiefly of the trunk and tail were obtained, and it was found that these movements could be modified by simultaneous stimulation of the cortex. This effect was not constant; it was usually of the nature of a partial inhibition, but sometimes the movement became better sustained although less in extent, and sometimes no effect could be detected.

Partial and complete removal of the hemispheres failed to demonstrate the localization of any precisely definable motor function in these parts of the brain. To some extent the experiments supported the idea that the striatum, and probably other basal centres, function as coordinating mechanisms in the synthesis of motor behaviour patterns, e.g. the feeding activities. They suggest that these centres participate in the control of muscular tone, and that they can facilitate or inhibit motor reactions in lower levels of the nervous system.

None of these experiments gives any support to the theory that the antero-dorsal part of the cerebral cortex of reptiles is neopallial in nature.

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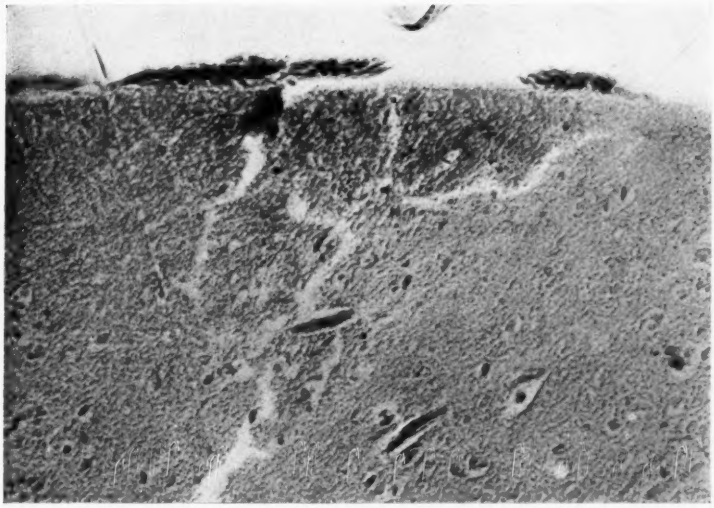

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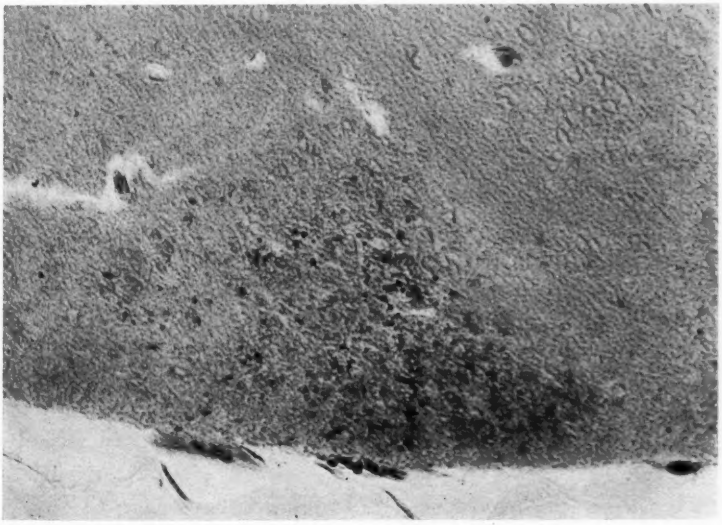

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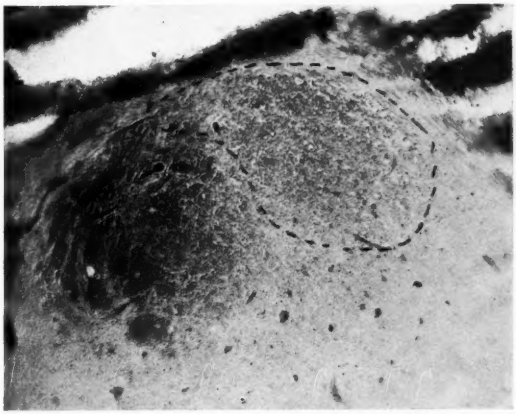

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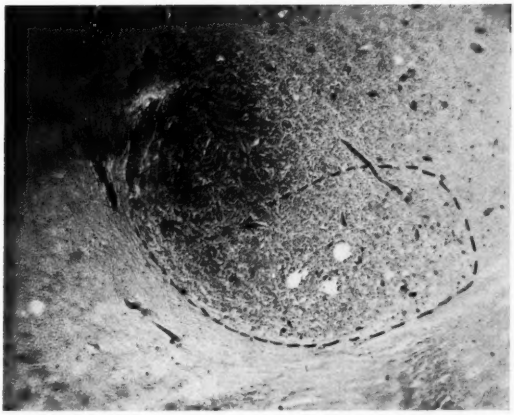

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EXPLANATION OF PLATES I AND II

Plate I

Lizard XVI. Photographs of the lateral olfactory tracts, A, from the degenerated, and B, from the normal side. Both photographs were taken from the same section which is drawn in outline in Text-fig. 3 (p. 335). The areas photographed have been marked in this figure.

Plate II

Lizard XXXI. Photographs of the forebrain bundles in the subthalamic region, A, from the degenerated, B, from the normal side. The area covered by the ventral peduncle of the combined forebrain bundles is surrounded by a dotted line. Text-fig. 10 (p. 342) is a drawing of the section from which these photographs were taken, and the area covered by them is marked on it. For a description of the degenerative changes shown, see the text (p. 341).

ABBREVIATIONS USED IN THE FIGURES

Key to lettering

B. Olf.	Bulbus olfactorius.	*Med.*	Medulla.
B. Olf. Acc.	Bulbus olfactorius accessorius.	*N. Olf. Ant.*	Nucleus olfactorius anterior.
Bas. Opt. Rt.	Basal optic root.	*Palst.*	Palaeostriatum.
Cereb.	Cerebellum.	*Ped. Olf.*	Pedunculus olfactorius.
Com. Post.	Commissura posterior.	*Ped. Dor.*	Pedunculus dorsalis.
Cx. Dor.	Cortex dorsalis.	*Ped. Vent.*	Pedunculus ventralis.
Cx. Hip.	Cortex hippocampi.	*Prim. Neop.*	Primordium neopallii.
Cx. Hip. (*L.C.*)	Cortex hippocampi, large celled part.	*Sept.*	Septum (paraterminal body).
Cx. Hip. (*S.C.*)	Cortex hippocampi, small celled part.	*Tect. Opt.*	Tectum opticum.
Cx. Pyr.	Cortex pyriformis.	*Thal.*	Thalamus.
Fs. End.	Fissura endorhinalis.	*Tr. Olf. Lat.*	Tractus olfactorius lateralis.
Hyp.	Hypopallium.	*Tr. Opt.*	Tractus opticus.
Hypoth.	Hypothalamus.	*Tub. Olf.*	Tuberculum olfactorium.
L.F.B.	Lateral forebrain bundle.	*Vent. III.*	IIIrd ventricle.

THE NARIAL MARGINS IN MAN

By EDWIN H. JOHNSON
Department of Anatomy, University of Melbourne

Up to the present time no theory has been advanced to account for the variations in the form of the narial margins to which attention has so frequently been drawn in descriptive physical anthropology. For the correct appreciation of the factors involved, it is obviously essential that the development and structure of the bones forming the narial margins should be understood.

During an investigation into the controversial question of the development of the premaxilla, certain significant features were observed which, it is thought, offer an explanation of the varying conditions met with. In this communication, a résumé of the findings will be given, and the theory relating to the variations of the narial margins to which they gave rise subjected to examination.

In 1869, Callender described what he termed the "incisor processes of the maxillae", which extended medially from the body of the maxillae and covered the premaxillae on their facial aspect.

Prof. Wood-Jones in 1914, unaware of Callender's work, concluded, after examining Prof. Fawcett's collection of developing chondrocrania, that "when the human embryo is no more than 19 mm. long, the premaxilla is losing its identity in the cartilage of the maxilla, and when the embryo is another 5 mm. longer, it has ceased to exist as a separate entity on the face". "The human premaxilla is lost in, and becomes overgrown by, the facial portion of the maxilla, but it still shows its independence of the maxilla, not only upon the palate, but within the nasal chambers."

Further confirmation of Callender's findings has been given by Ashley-Montagu in his paper, "The premaxilla in the primates".

At Prof. Wood-Jones's suggestion, the present writer made an examination of a number of white foetuses of various ages in an endeavour to determine the maxillary-premaxillary relationship in man.

In all the specimens dissected, the only trace of the premaxilla to be seen on the face was in the region of the inferior margin of the narial aperture.

In a foetus of 3 months (Fig. 1), traces of a suture, or rather a deficiency in the bone, were noticed between the outer and inner alveolar walls of the central and lateral incisors. This suture extended from the medial border of the canine socket, between the outer and inner alveolar walls, medially and anteriorly towards the anterior nasal spine. Confirmation of the presence of this suture was found in other foetuses between 3 and 4 months, but in later specimens, owing to the growth of the alveolar bone in the sockets, it was not discernible.

The apparent explanation is that the maxilla has grown forward and formed the anterior walls of the sockets of the incisor teeth, though this forward growth has not taken place in the region of the nasal spine.

Jarmer, associated with Karl Peter, also describes and figures this suture, which he terms the "interalveolar suture", but he ascribes the anterior (facial) part of the bone to a separate ossification centre of the premaxilla rather than to an extension of the maxilla itself.

In a foetus of 6½ months (Fig. 2), I found that in the region of the inferior margin of the narial aperture the maxilla had not completely covered the premaxilla. The lateral margin is formed by the anterior edge of the maxilla, but, as is shown in Fig. 2, its lower border has merged into the superior alveolus at the inferior lateral angle of the narial aperture.

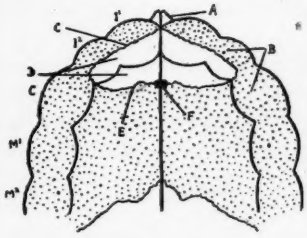

Fig. 1.

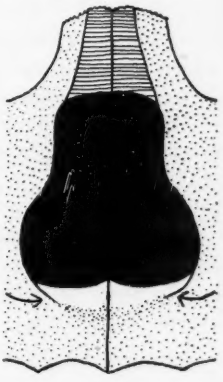

Fig. 2.

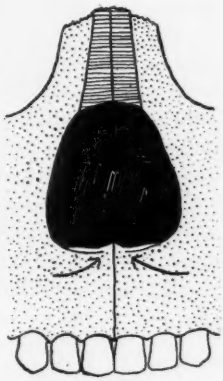

Fig. 3.

Fig. 1. Palatal view of a 3 months' foetus showing interalveolar suture, the anterior walls of incisor sockets being formed by the maxillae.

A, anterior nasal spine; *B*, maxilla; *C*, interalveolar suture; *D*, premaxilla; *E*, incisive suture; *F*, anterior palatine foramen.

Fig. 2. The narial margins in a foetus of 6½ months showing maxillary overlap of the premaxilla.

Fig. 3. Showing maxillary overlap almost complete in a child of 5 years.

Posteriorly, and separated by a sulcus from the maxillary margin, the anterior edge of the premaxilla may be seen passing from the nasal spine laterally along the floor of the nasal fossa on to the nasal surface of the maxilla, up which it extends as far as the ridge for the inferior concha, lying in its course some little distance posterior to the maxillary margin.

In the skull of an infant of 5 years, it is seen that the maxilla has grown farther forward towards the nasal spine, although the inner or premaxillary ridge is still apparent.

In the adult white skull (Fig. 7), there is usually a single sharp narial margin, the result of the maxilla having completely overgrown the premaxilla, leaving, as a rule, no trace of the double margin of the foetus.

Thus, in summarizing the ontogenetic development, it is seen that, as early as the 24-mm. stage, the premaxilla is becoming merged into the maxilla. In the 3 months' foetus, the incisor process of the maxilla has overlapped the premaxilla facially, forming the anterior walls of the incisor sockets. Later, farther forward growth of the maxilla results in the formation of a double inferior narial margin as seen in the 6½ months' foetus, where the anterior margin is formed by the maxilla and the posterior by the premaxilla. The premaxilla, however, is still distinct in the region of the nasal spine. At a later stage, 5 years, the maxillary component of the inferior narial margin has merged into the premaxillary, although the two ridges are still observable. In the adult white, the culmination of the process is seen in the single sharp narial margin formed by the maxilla which has completely overgrown the premaxilla.

The suggestion arising from these findings is that the duplication of the inferior narial margin, which is such a feature in certain skulls, is due to an incomplete passage of the incisor processes of the maxillae forwards, so that, although they still meet in the median line and form the anterior walls of the incisor sockets, they do not divorce the premaxillae from entering into the formation of the narial margin.

Von Baer has stated that "the less general structural relations are formed after the more general, and so on until the most special appears". If we apply this dictum to the present case, we may say that the early fusion of the maxilla and premaxilla is evidence of early phylogenetic acquirement, and that the double narial margin, culminating in the single sharp margin so late in ontogeny, is evidence of a later phylogenetic initiation.

It will be interesting, therefore, to examine first the narial margin in the nonhuman primates.

THE NARIAL MARGIN IN THE PRIMATES

As the facial sutures in most of the nonhuman primates remain open for long periods, or even throughout life, it is an easy matter to determine the anatomy of the narial aperture. This is formed by the nasals above, and laterally and inferiorly by the premaxillae.

If a prognathous type, such as a macaque (Fig. 4), is examined, it will be seen that the maxillary-premaxillary suture passes between the lateral incisor and canine and then directly upwards towards the nasals. The maxilla shows none of the "embracing" effect as in man.

In the gorilla (Fig. 5), however, a most interesting condition is noticed, for in this animal, probably the least prognathous of the anthropoids, the suture, after passing from the palate between the lateral incisor and canine, divides the septum between these two and then sweeps medially, emerging on the face at a point over the middle of the lateral incisor socket. It then progresses

farther medially, so that, in its upward course on the face, the suture lies over the premaxilla as far as the distal septal wall of the upper central incisor.

Thus, compared with the macaque, a decrease of subnasal prognathism is associated with the forward growth of the maxilla to cover, in part, the facial aspect of the premaxilla.

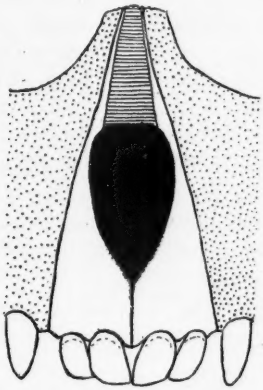

Fig. 4. Narial margins of macaque formed by the premaxillae.

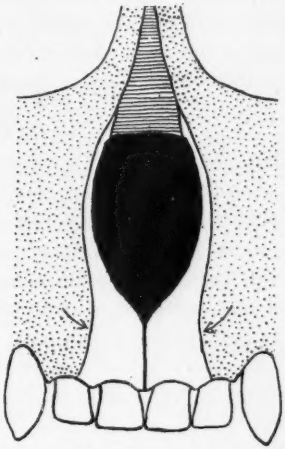

Fig. 5. Maxillary overlap of premaxilla in gorilla.

Fig. 6. Double inferior narial margin of Australian aborigine, formed by premaxilla and maxilla.

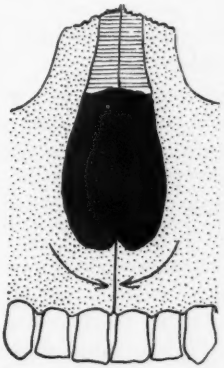

Fig. 7. Maxillary single narial margin of white adult.

Observations made on the ontogeny of the maxilla and premaxilla in man, and on their changing relationship in the primates, support the statement that the incisor processes of the maxillae are overgrowing the premaxillae in phylogeny.

THE HUMAN NARIAL MARGIN

If the skulls of various races be examined, differences will be noticed in the types of narial margins. Prof. Wood-Jones says of the prehistoric inhabitants of Guam that "the narial margins are practically always double, with low ridges and considerable separation. The divergence of the margins in 23 per cent and the continuity between the superior alveolar surface and the floor of the nasal chamber reaches the condition that is best described as guttered. In only 7 per cent were the margins approaching the condition that can be termed sharp and these more sharply marked margins were all present in the skulls of women. There is a conspicuous degree of apparent subnasal prognathism in the typical skull."

Wilton M. Krogman thus described the narial aperture of the Australian aborigine (Fig. 6): "The narial margins are usually double and in 16 per cent of the males and 3 per cent of the females a fossa prenasalis is to be observed. As a rule the inferior nasal margin is not sharply delineated but slopes down to the alveolar portion of the maxilla. Subnasal prognathism is present in both males and females to quite a marked degree."

These observations are in agreement with those I have made of the collection of Australian skulls at the Department of Anatomy Melbourne University.

Of the Hawaiians, Wood-Jones says: "The narial margins are typically double. Both margins are, as a rule, well defined and the outer margin tends to be sharper and more distinct than the inner. A single sharp margin was found in 8 per cent and was three times as numerous in women as in men. Apparent subnasal prognathism is generally evident, but it is of a slight or only moderate degree."

In the white skull, as I have stated, the margin is usually sharp and single with prominent nasal spine, whilst the face is orthognathous.

That these variations of the narial margins are in accord with the degree of subnasal prognathism present there seems but little doubt. The explanation then is that in the phylogenetic development of man there has occurred a reduction in the size of the premaxilla. The widely separated narial margins of the Australian aborigine, in which the outer margin merges into the superior alveolus, is evidence that the maxilla has failed to overgrow the premaxilla completely. In the Hawaiian skulls, the degree of ingrowing of the incisor process of the maxilla has advanced a stage farther with the lesser degree of subnasal prognathism, whilst in the adult white the premaxilla has been completely shut off from the face.

Thus we have seen that in the nonhuman primates the narial margins are completely premaxillary—in the prognathous types of man the margins are formed by the maxilla and premaxilla in degree varying according to the amount of subnasal prognathism—whilst, in the orthognathous white, the narial margins are completely maxillary.

I take this opportunity of expressing my indebtedness to Prof. Wood-Jones for suggesting the subject of my investigations and for providing facilities and material for carrying out the work. To him also are my thanks due for his kindly assistance in reading this paper in manuscript and in the preparation of the diagrams. To Drs E. Ford and S. Sunderland, I acknowledge much friendly advice and help.

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ON THE CHEEK-BONES IN TELEOSTOME FISHES

By T. S. WESTOLL, B.Sc., Ph.D.
Department of Zoology, University College, London

This study was prompted by observations on the cheek-bones of certain Palaeoniscid and Holostean Fishes, which suggested that a more definite answer could now be given to the unsatisfactory problem of the homology of the bones of the cheek in certain Fishes. The examination of further material confirmed this view, and the body of evidence collected, though no doubt very incomplete, seems to be sufficient for a coherent account of the fate of certain cheek-bones during the long geological history of the Fishes.

While gathering this evidence during the past year or two the writer has made observations on fossil Fishes belonging to many museums and institutes: in particular he desires to thank Mr C. Forster Cooper, M.A. (University Museum of Zoology, Cambridge), Mr T. Russell Goddard, M.Sc., F.L.S. (Hancock Museum, Newcastle-on-Tyne), Dr J. Piveteau (Paris), Dr A. C. Stephen (Royal Scottish Museum, Edinburgh), and Prof. D'Arcy W. Thompson (University Museum of Zoology, St Andrews) for allowing him to study and borrow so much material. Prof. E. A. Stensiö, Dr G. Säve-Söderbergh, Dr H. Aldinger and Dr E. Nielsen were very kind in showing me much pertinent material, some of it yet unpublished, which forms part of the splendid collections from East Greenland and Spitzbergen preserved in the Riksmuseum, Stockholm, and at Upsala, and I wish to thank them for these and many other courtesies. The work was begun while investigating the English Permian Palaeoniscids under the supervision of Prof. G. Hickling, F.G.S., to whom I am deeply indebted for constant kindness and encouragement. It has been continued in London, and I desire to thank Dr E. I. White, F.G.S., and the authorities of the Natural History Museum for allowing me the full use of the magnificent fossil fish collections there. I can only acknowledge in small part the great debt which I owe to Prof. D. M. S. Watson, F.R.S., who has continuously translated his interest in the writer's palaeontological research into active help and acute criticism. Finally, I wish to thank the Department of Scientific and Industrial Research for a Senior Research Award, without which this and other work could not have been attempted.

STATEMENT OF PROBLEM

The determination of the true homologue of the mammalian squamosal in the very primitive Tetrapods was for long a vexed question, and only in recent years has it been clearly demonstrated that the bone is represented in the cheek as a dermal plate associated, in the most primitive forms, with the

horizontal part of the jugal canal or its equivalent "slime-groove" (nomenclature stabilised by Säve-Söderbergh, 1933, p. 7). The equivalent of this bone in a Rhipidistian such as *Osteolepis* is easily distinguished, and has, in general, the same geographical and anatomical relationships. This provides us with a starting-point for a discussion of the piscine cheek.

It will be unnecessary to discuss here the historical differences of opinion about the position of the squamosal in lower Tetrapods and primitive Fishes, as we are concerned with the fate of the squamosal, quadratojugal and pre-opercular, as defined, for example in Säve-Söderbergh's account of *Osteolepis* (*op. cit.*).

Since the recognition of the true squamosal in Fishes there have been few definite opinions expressed on the fate of that bone in the "higher" Fishes. Stensiö (1921, p. 139), however, in a characteristically cautious passage, has stated most of the possibilities, according to his views on the nature of the Rhipidistian squamosal. He suggests that the squamosal in Crossopterygians may really be derived from a number of rudiments fused together, and goes on: "One may venture the supposition that all the homologues of the elements forming the squamosal in the Rhipidistids have never been fused with one another into one bone-plate in the Actinopterygians, but that they were either distributed among the surrounding bones, or with partial modifications had been fused into certain larger units which afterwards preserved their mutual independence or else were finally more and more reduced. In the Palaeoniscids, Platysomids and Catopterids it is conceivable that the original squamosal elements were divided up between the maxillary and the pre-opercular, and that they have even provided material for the so-called post-orbitals. In certain Protospondyli, such as the Semionotids and Eugnathids, they all probably provided material for the majority of the so-called post-orbitals (suborbitals); the ventral one, or some of them, can probably, as we have seen, be considered as corresponding to the quadratojugal: in the Teleosts the homologues of the squamosal elements usually seem to be reduced. Sometimes, however, it seems possible that parts of them may persist in the plates of the infra-orbital chain, in the cases when these plates are much developed and cover the cheek between the orbit and the pre-opercular to any great extent."

Säve-Söderbergh (1934, p. 14), when comparing Crossopterygians with Actinopterygians, has adopted a very interesting point of view. "The dermal bones of the cheeks are certainly not simply homologous, or even easily comparable in the two groups....After all, it seems perhaps most probable that the pattern of dermal bones of the *Choanata* and that of the Actinopterygians have evolved quite independently from ancestors with either a very high number of bones—a mosaic—or with a more or less undivided dermal covering of the head."

The writer's work on fossil Fishes has convinced him that the ancestors of the Choanata and Actinopterygians had, in times not much earlier than

the first known appearance of those groups, a mosaic of dermal bones covering the head, and that the sensory organs of the lateral line system were each related to a dermal bone. The examination of Dipnoans and Crossopterygians has made it clear to him, moreover, that many of the larger bones found in the skull of known Fishes are due to coalescence of the lateral line units, with growth of these elements at the expense of the "anamestic" bones between (Westoll, 1936), and not to indiscriminate fusion of plates of the original mosaic. The sensory organs of the lateral line system appear to the author to be of very great importance in determining the position of dermal bones in the primitive Fishes, and have allowed a new interpretation of the cheek to be made.

In the following account the conditions in the various groups of Fishes will be described, followed by a discussion of the results in the light of what has been said above.

CROSSOPTERYGII

The cheek-bones of *Osteolepis* correspond so closely with those of an Ichthyostegid or *Eogyrinus* that there can be no doubt of individual homologies (fig. 1 A and B). The main morphological distinctions are: (i) the binding of the cheek-bones to the skull roof in Tetrapods, and (ii) the broad contact between squamosal and maxillary in *Osteolepis* (not found, however, in some Rhipidistia).

The latter point is not of great importance, as it is probably due only to the excessive backward extension of the cheek in *Osteolepis*. The important anatomical similarity is the fact that the squamosal is pierced by the jugal canal of the lateral line system: in *Osteolepis* the squamosal is also associated with the dorsal part of the vertical cheek-line of pit-organs. The jugal canal passes backwards into the short vertical pre-opercular canal, and passes forwards to anastomose with the infra-orbital canal in the jugal. The distribution of the other bones is well shown in fig. 1 B. This typical arrangement is only slightly modified in most other Rhipidistia (e.g. *Diplopterax*, *Thursius*, *Megalichthys*, *Eusthenopteron*, etc.[1]), but frequently a continuous sheet of cosmine covers squamosal and quadratojugal, although the bones are separate (cf. Westoll, 1936).

The conditions in *Holoptychius*, however, are more complex (fig. 1 C). The structure can be made out admirably in *H. flemingi* from Dura Den, and the figure is derived from specimens at St Andrews. The cheek is comparatively much longer than in *Osteolepis*, and, probably because of the large size of the squamosal even in that fish, it appears that a single growth centre proved inadequate to cover a larger cheek. The consequence is that there are two squamosal bones, and two small bones have been necessary to fill space: these are of the type for which the author has proposed the name anamestic (Westoll, *loc. cit.*). The pre-opercular has been pushed backwards and has divided the bones of the opercular folds into two series. The structure will not be further

[1] Author's observations.

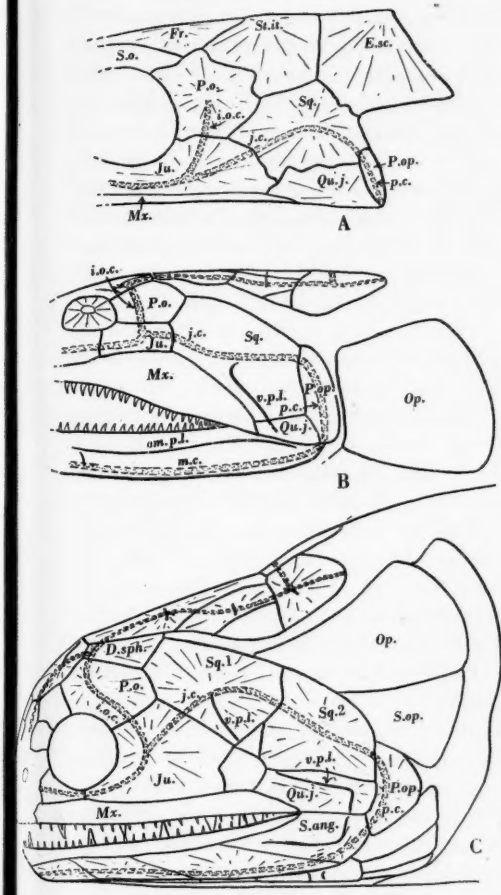

Fig. 1.

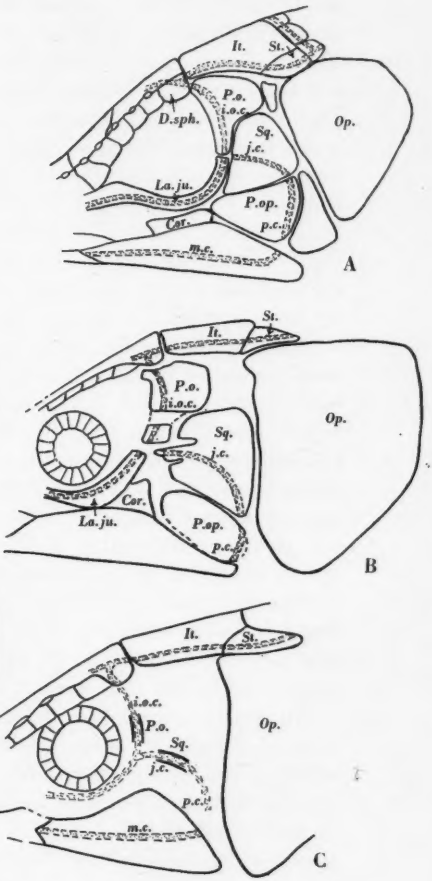

Fig. 2.

Fig. 1. A. Cheek of Ichthyostegid, mainly from *Ichthyostegopsis wimani* S.-S. After Säve-Söderbergh. B. Cheek of *Osteolepis macrolepidotus* Ag. After Säve-Söderbergh. C. Cheek of *Holoptychius flemingi*. Drawn from material at St Andrew's University Museum of Zoology.

Fig. 2. A. Cheek of *Whiteia* (Lower Trias, Madagascar). After Moy-Thomas, additions by author. B. Cheek of *Wimania sinuosa* Stensiö. After Stensiö. C. Cheek of *Axelia robusta* Stensiö. After Stensiö.

described here, as Dr G. Säve-Söderbergh is to deal with the structure of *Holoptychius* in detail.

Turning now to the Coelacanths, we find more divergence. The cheek of the Devonian forms is, unfortunately, unknown. In most other Coelacanths from various geological formations the cheek has quite a characteristic aspect. The infra-orbital canal leaves the skull roof and traverses a broad post-orbital and then a very long bone called lacrimo-jugal. The jugal canal appears to anastomose with the infra-orbital at the junction between these bones, and passes backwards through a large bone which we may confidently homologise with the squamosal. It then passes more or less abruptly into a vertical canal which traverses the hinder margin of a bone of usually somewhat smaller size lying postero-ventrally to the squamosal and called "preoperculo-quadratojugal" (Stensiö) or "quadratojugal" (Moy-Thomas). Between the post-orbital, the skull roof and the opercular, is often a small bone called "suprasquamosal" by Stensiö (1932, p. 43) and Moy-Thomas (1935, p. 218), and behind the "quadratojugal" of the latter, and below the opercular, is a bone which has been recognised only by Moy-Thomas, and which he has termed "pre-opercular". This structure is known in Carboniferous forms (*Coelacanthus elegans* Newb., Moy-Thomas, 1935, fig. 10), in a new form from the Permian of Texas (author's unpublished observations), in certain Triassic forms (*Coelacanthus madagascariensis*[1] M.-T., and *Whiteia*[1] M.-T., Moy-Thomas, *op. cit.*, see fig. 2 *a*, and some types from East Greenland shown to the writer by Dr E. Nielsen) and in the Cretaceous form *Macropoma* (Watson, 1921, fig. 5). Few other species have been described in sufficient detail to be of value in this discussion. *Coelacanthus watsoni* (Aldinger, 1931, fig. 2) from the Carboniferous of Westphalia is incompletely known in this region, as is *Laugia* from the Greenland Eotrias (Stensiö, 1932, p. 46, fig. 19), though in the latter case Stensiö has suggested that the "preoperculo-quadratojugal" is not developed.

In certain genera from the Triassic of Spitzbergen the cheek-bones seem to be much reduced. *Wimania sinuosa* may show the beginnings of this process, which is apparently carried very far in *Axelia robusta* (Stensiö, 1921) (see fig. 2 B and C). The writer has seen these fishes at Upsala, owing to Prof. Stensiö's kindness, and agrees that *Axelia* probably shows the results of extensive reduction of cheek-bones, only tubular ossifications round the sensory canals being preserved.

It remains only to discuss the nature of the "preoperculo-quadratojugal" (Stensiö) or "quadratojugal" (Moy-Thomas, and Stensiö in certain cases). In the only cases in which the course of the sensory canal is known, it passes vertically through the hinder part of the bone (the unpublished Texan Permian genus, *Whiteia*, *Macropoma*, all from author's observations, and in several East Greenland types kindly shown me by Dr Nielsen). Moreover, in the Carboni-

[1] Both Mr Moy-Thomas and the writer have seen that the sensory canal in the cheek traverses the bone called "quadratojugal", and not that called "pre-opercular" in these Fishes by the former.

ferous and Permian forms so far known in detail, the bone does not extend far forwards (*Coelacanthus elegans* Newb., *C. watsoni* Aldinger and the Texas Permian form), while in many Triassic types and in *Macropoma* it extends forwards to the lacrimo-jugal. It is probable, therefore, that this forward extension is a development within the group. The bone is therefore regarded by the writer as a pre-opercular, without any quadratojugal element. The small bone lying behind it (the "pre-opercular" of Moy-Thomas) I regard provisionally as a bone of the opercular fold. It is obvious that the whole structure of the cheek of a Coelacanth must have been profoundly modified by the loss of the maxillary when compared with a Rhipidistian: that the Coelacanths were actually derived from a Rhipidistian seems well established. Consequently the writer does not believe that the forward extension of the pre-opercular is evidence for the existence of a quadratojugal component.

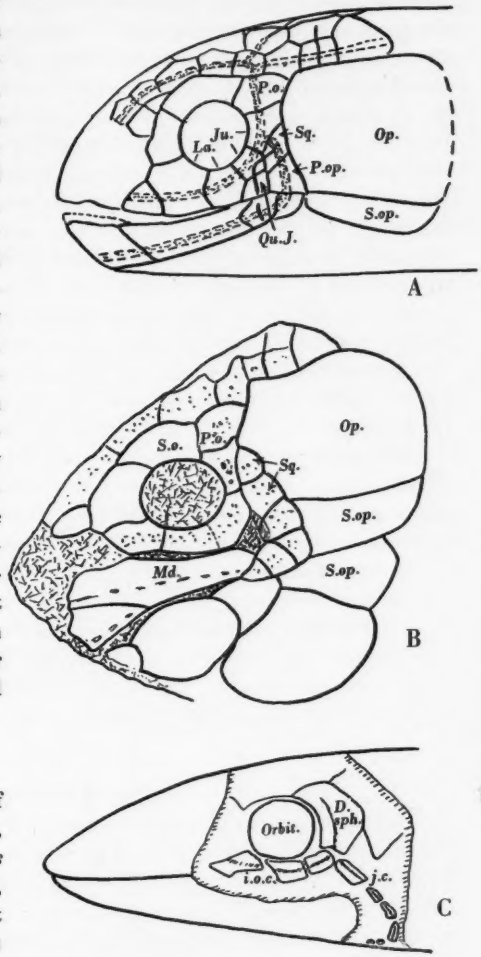

Fig. 3. A. Cheek of *Dipterus valenciennesi* Ag. from material collected at Achanarras by Dr C. Forster-Cooper. B. Cheek of *Scaumenacia curta* (Whiteaves). Drawing of a specimen belonging to Mr W. Graham-Smith. C. Cheek of *Ceratodus* (*Neoceratodus*) *forsteri*. After Fürbringer.

DIPNOI

The structure of the cheek of fossil Dipnoi has been known, very partially, only in *Dipterus* and *Sagenodus* (Watson and Gill, 1923). However, during recent examination of many members of the group the writer has been able to see much of the cheek of *Scaumenacia*, and to study in some detail that of *Dipterus*.

In *Dipterus* (fig. 3 A) the cheek shows a certain amount of variation in detail, but the general plan is constant. The post-orbital is followed by two bones lying behind and below the eye, which correspond together in position

with the jugal of *Osteolepis*. Between these bones and the opercular is a triangular space occupied by three or four bones, the disposition of which will be clear from the figure. There is a sensory canal—obviously homologous with the jugal and pre-opercular canals of Rhipidistia—which traverses the two or three bones lying next to the opercular. The antero-ventral plate, not associated with the sensory canal, is related to the ventral end of a pit-line groove which curls upwards on to the uppermost cheek-bone: it may or may not pass over the jugal (circumorbital) elements. These circumstances make it clear that the antero-ventral plate is the homologue of the quadratojugal, and that the other two (or three) plates correspond with the squamosal and pre-opercular. In the cases with three such plates the uppermost plate may provisionally be called squamosal, the lower members pre-opercular. The extra compression of this region is due to the forward passage of the suspensorium, the reasons for which, together with a discussion of the relationship between *Dipnoi* and Crossopterygii, are reserved for treatment on another occasion. This account is based on the examination of a great series of fossils collected by Mr Forster-Cooper at Achanarras, and has only been made possible by his generosity in allowing me to study the material.

The cheek of *Scaumenacia* is essentially similar (fig. 3 B): there is no quadratojugal in this specimen but there is a lacuna in the appropriate position. The drawing is based on a fine specimen from Scaumenac Bay collected by Mr Graham-Smith, B.A., to whom the writer is greatly indebted. In no other fossil Dipnoan is the cheek adequately known: only in *Sagenodus* is there any trace of a cheek-bone behind the circumorbital bones.

The existence of some tiny bony plates connected with the jugal canal in *Neoceratodus* was indicated by Fürbringer (1904, pl. 37–38, fig. 5), and the writer has corroborated this by observation on preserved material and on serial sections of larval specimens (fig. 3 C).

ACTINOPTERYGII

(*a*) *Palaeoniscoids*

The most primitive Actinopterygian yet known is *Cheirolepis trailli*, from the middle Old Red Sandstone. It has been described, with excellent figures, by Watson (1925), who, however, dealt only with the dermal bones of the outside of the skull. The writer has made new observations on the structure of the palate, mandible and cranium which will be published elsewhere: however, it may be noted that the structure is not so different from that of Osteolepids as is usually considered, and offers a very useful basis of discussion of the relationship of the two groups of Fishes. The cheek is covered by the expanded pre-opercular and maxillary; between them, postero-ventrally, is often some trace of a small bone, which has most of the relations of a quadratojugal. The pre-opercular canal runs almost the full length of the pre-opercular bone, not traversing the bone *Y* of Watson's figures, and emerges from the dorsal margin opposite the cleft between the post-frontal of Watson's figures

(really the post-orbital) and the bone *Y*. The bones called "post-orbital", "jugal", by Watson seem to the writer to correspond better to the jugal and lacrimal respectively of Rhipidistia. Unfortunately no trace of the horizontal cheek-line of pit-organs (corresponding to the jugal canal) has so far been observed. The bones *X* and *Y* are referred to the opercular system for the time being (fig. 4 A).

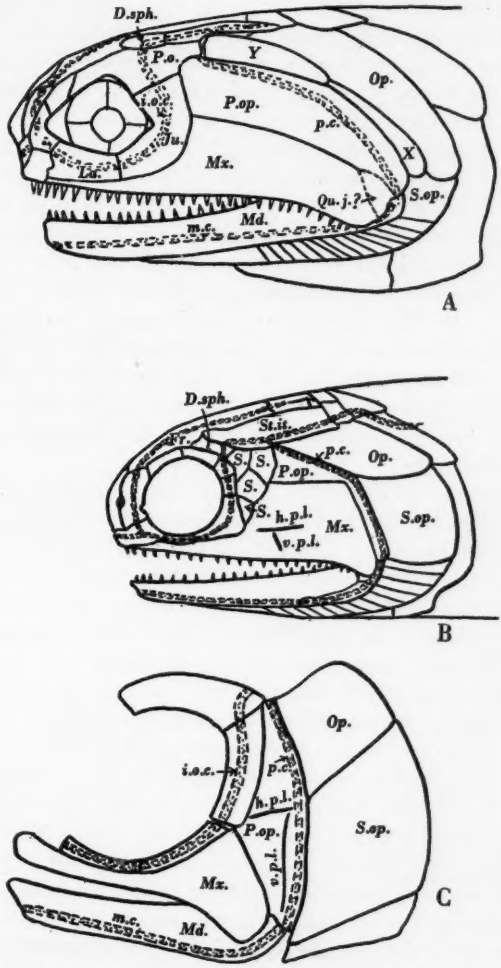

Fig. 4. A. Cheek of *Cheirolepis trailli* Ag. From Watson, with additions. B. Cheek of a hypothetical Palaeoniscid showing position and relations of bones and structures. C. Cheek of *Canobius* sp., from Cementstones of Eskdale. Drawn from material in Manchester, B.M.N.H., etc.; sketch only.

In later Palaeoniscid Fishes there are great variations in the details of the cheek, but generally speaking the area is covered by varying developments of the pre-opercular and the maxillary expansion, with, in many Carboniferous and later forms, a series of so-called "suborbital" plates lying behind the circumorbitals. As these latter are not found in *Cheirolepis* and *Stegotrachelus*, and are found very well developed in many later forms, they have probably arisen in the history of the group.

The relative size of the pre-opercular and maxillary varies over quite a wide range in the group, but there is never any suggestion that the difference may be due to the fusion of separate rudiments to one or the other bone. It is unfortunate that the development of the pit-lines of the cheek, corresponding to the jugal canal and vertical pit-line of Rhipidistia, is not capable of being studied in many forms, as these structures leave no mark on the cheek-bones in these cases. I have, however, been able to see a well-marked groove for the horizontal cheek-line of pit-organs in *Pygopterus humboldti* Ag., where it occurs on occasional specimens on the anterior part of the maxillary expansion, and traces of a similar groove have been observed on a few other "Palaeoniscids". Dr Eigil Nielsen has kindly shown the writer a vertical pit-line groove low down on the maxillary expansion of another Palaeoniscid from the East Greenland Eotrias.[1] All of these genera have rather high, well-marked maxillary expansions: the figure (fig. 4 B) shows the general relationship of pit-line grooves, sensory canals and cheek-bones in a composite, imaginary Palaeoniscid.

The small Fishes *Canobius* (from the Cementstones of Eskdale, Dumfriesshire) and *Eurylepis* (from the Coal Measures of Ohio and England) have a vertically or even forwardly directed suspensorium, and the pre-opercular forms the greater part of the cheek. In these forms the horizontal and vertical pit-lines are on the pre-opercular expansion (see fig. 4 C). These Fishes will be described in detail by Dr E. I. White and the writer respectively.[2]

Of the Palaeoniscid derivatives, the Saurichthyids are of great interest. These fishes have long snouts and extremely oblique suspensoria, no doubt related to the habits of life: *Saurichthys hamiltoni* Stensiö (Stensiö, 1925, fig. 54, pl. 27) shows the conditions very well (fig. 5 A). The cheek behind the circumorbitals is covered by three bones, called maxillary, pre-operculum and quadratojugal by Stensiö. The growth centre of the "quadratojugal" is far posterior, and judging from the conditions in other species (*S. ornatus*, *op. cit.*, fig. 21; *S. wimani*, *ibid.*, fig. 42; *S. elongatus*, *ibid.*, fig. 46) it is perforated by the pre-opercular sensory canal: the writer believes this to be so after examining the type material at Upsala, and prefers to regard the bone as a separated part of the pre-opercular. The condition may be compared with the divided squamosal in *Holoptychius*, due to the elongation of the cheek.

[1] But see postscriptum! (p. 382).

[2] Short grooves for the horizontal and vertical pit-lines occur on the pre-opercular of a few specimens of *Diaphorognathus* sp. from the Eotrias of Madagascar: this is a "normal" Palaeoniscid with a very slightly expanded pre-opercular.

Cleithrolepis granulata Egerton (Wade, 1935, p. 49, fig. 23) has recently been shown to have a deep cheek covered by the maxillary, pre-opercular and a small bone called the quadratojugal, but bearing the pre-opercular sensory canal: this bone is better regarded as a separated portion of the pre-opercular, as in the last case (fig. 5 B).

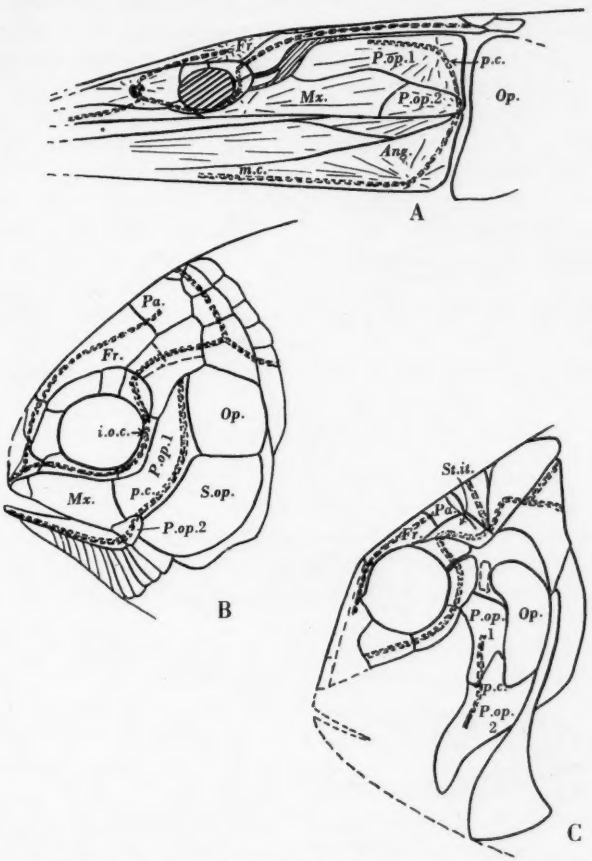

Fig. 5. A. Cheek of *Saurichthys*, mainly from *S. hamiltoni*, Stensiö. After Stensiö. B. Cheek of *Cleithrolepis granulata* Egerton. After Wade. C. Cheek of *Bobasatrania groenlandica* Stensiö. After Stensiö.

In other deep-bodied Palaeoniscid derivatives the conditions are not known with complete certainty: but the pre-opercular is apparently rather often divided into a dorsal and a more ventral part, a feature correlated with the great deepening of the cheek. The conditions in *Bobasatrania* are illustrated in fig. 5 C: the fish is described by White and Stensiö (White, 1932, and

Stensiö, 1932, p. 127). The writer's observations on Platysomids are unpublished, but it is probable that somewhat similar conditions hold in certain members of this group.

In the very numerous Triassic Palaeoniscid derivatives (Perleidids, Catopterids, Parasemionotids, etc.) the pre-opercular usually plays a larger part

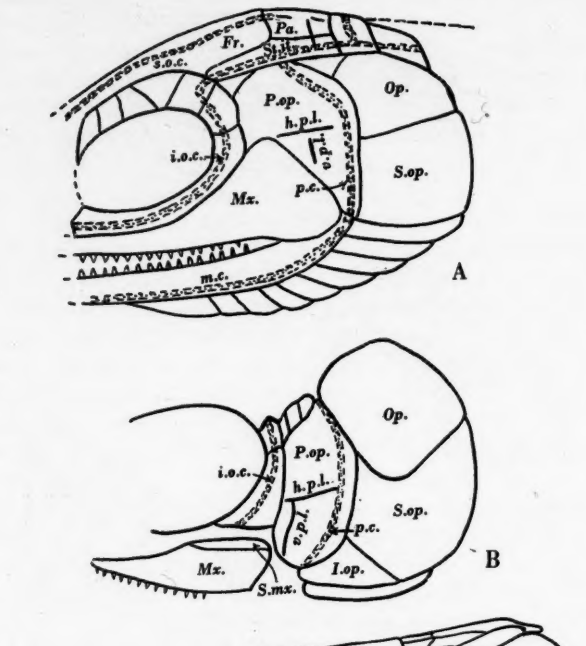

Fig. 6. A. Cheek of *Perleidus madagascariensis* Piveteau. After Piveteau, with position of cheek pit-lines in this and other species added. B. Cheek of *Parasemionotus labordei* Piveteau After Piveteau. C. Cheek of *Polypterus*. After Allis.

in the cheek than in the earlier forms, particularly in the Perleidids. Piveteau has recorded a groove for the horizontal pit-line on the pre-opercular of *Perleidus madagascariensis* (Piveteau, 1934, p. 47), and the writer has found traces of the vertical pit-line on the same bone in the type of *P. woodwardi* (Stensiö, 1921, pl. 33), preserved at Upsala (fig. 6 A). In the Parasemionotids,

Piveteau has figured the horizontal and vertical pit-line grooves on the pre-opercular in *Watsonia* (*op. cit.*, figs. 42, 43) and *Parasemionotus* (*ibid.*, fig. 48) (fig. 6 B). In the Parasemionotids the maxillary has become free, much as in Holostei.

Polypterus has recently been considered a Palaeoniscid derivative by Goodrich (1928), and the writer regards Stensiö's suggestion (1921, p. 147) that *Polypterus* should be regarded as lying between the Crossopterygii and Actinopterygii as less in accord with the known facts. In this fish the cheek behind the circumorbitals is covered by a large plate which is part of the pre-opercular. In the most complete description of this fish (Allis, 1922, p. 238) this is named simply cheek-plate, and Allis suggests that it contains the homologues of squamosal and pre-opercular. There is, however, no evidence that the bone arises from two rudiments. The cheek-plate bears deep grooves for the horizontal and vertical cheek-lines of pit-organs. The writer suggests that the name pre-opercular is more truly descriptive of the plate than any compound name, in view of the similarity to *Watsonia*, *Parasemionotus*, *Canobius*, etc. It is very doubtful whether the scale-like bones situated below the cheek-plate have any historical importance, but they may correspond in a general way with the quadratojugal (fig. 6 C): they are far more likely to be neomorphs.

"HOLOSTEI"

In most of the Fishes hitherto considered the cheek is nearly completely covered by dermal bones, and the grooves for the pit-lines of the cheek are often well marked on the surface of the bones: in a number of Mesozoic ganoids the same conditions are found, but in some the bones seem to have been so far below the surface during life that the pit-lines leave no surface marks on them.

Well-marked grooves for the cheek-lines of pit-organs can be seen in most well-preserved specimens of *Lepidotus semiserratus* from the Upper Lias of Whitby. These occur on different members of the second row of plates behind the eye—the so-called "suborbitals" (fig. 7 A). The deeper bodied Semionotid fish *Dapedius* is similar, but there is no trace of the groove for the horizontal pit-line in any of the material I have seen. The dotted lines in the specimen of *D. colei* figured by Smith Woodward (1895, fig. 27, p. 141) extending from circumorbital plates on to separate "suborbitals" are cracks: the vertical pit-line is on the most anterior "suborbital", and is indicated in the figure cited above as a short line just in front of the broken line. On other specimens (e.g. P. 1559, British Museum, Nat. Hist.) the vertical pit-line extends from the most anterior "suborbital" upwards on to the adjacent infra-orbital plate (fig. 7 B).

There is little doubt that *Lepidosteus* is related to the Semionotid fishes: here the cheek between the circumorbitals and the pre-operculum is covered by a mosaic of small dermal bones. A few skulls, both of the sharp-snouted

L. osseus and of the "alligator gar", *L. viridis*, show the track of the horizontal cheek-line of pit-organs as separate grooves on the row of cheek-plates immediately above the horizontal limb of the pre-opercular, and recently examination of larval *Lepidosteus* by my friend Mr F. J. Aumonier, B.Sc., has con-

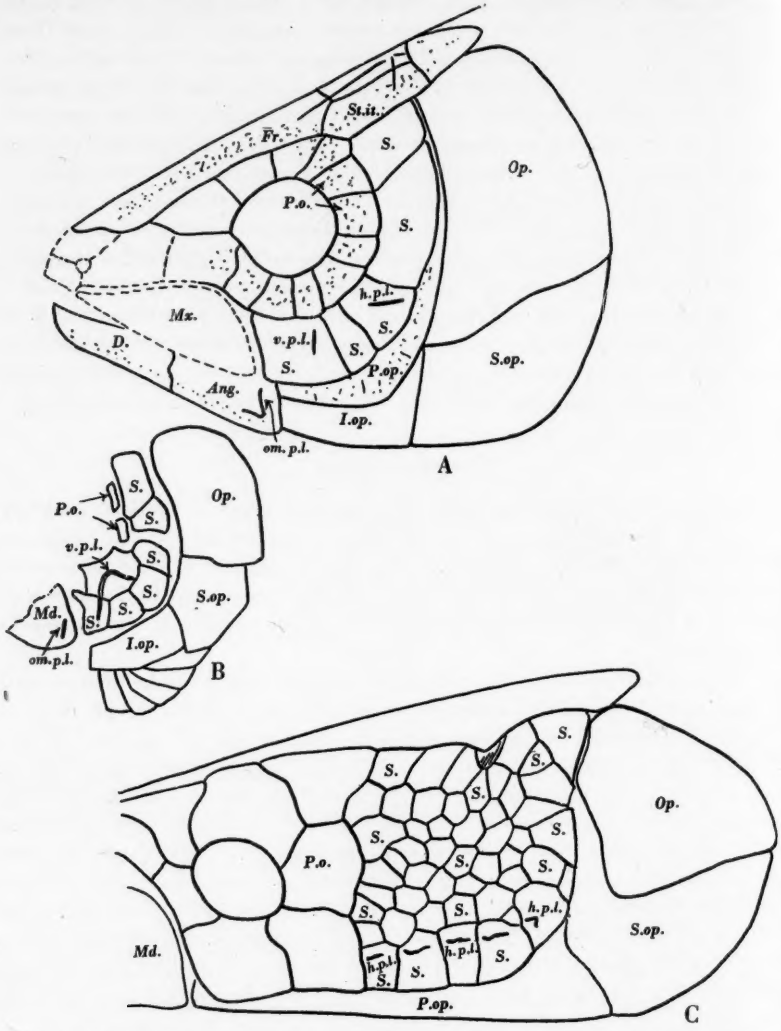

Fig. 7. A. Cheek of *Lepidotus semiserratus* Ag. From specimen in Hancock Museum, Newcastle-on-Tyne. Upper Lias, Whitby. B. Cheek of *Dapedius* sp. From P. 1559, B.M.N.H., Lower Lias, Lyme Regis. C. Cheek of *Lepidosteus viridis*. From specimen in Zoology Department, University College, London.

firmed this. The mosaic of cheek-plates seems to be undoubtedly a great development of the "suborbital" series (fig. 7 C).

Sharply distinct from this type of cheek is that found in many other Mesozoic "ganoids" (e.g. *Eugnathus*, *Caturus*, *Hypsocormus*, *Pachycormus*, etc.) in which the pre-opercular and circumorbitals are still narrow, but the intervening space is filled by a few large bones rather than by a number of small ones.

The family Eugnathidae is usually believed to be ancestral, in a general way, to the Amiidae. In *Eugnathus*, the cheek behind the post-orbitals is formed of a couple of large "suborbitals". On the magnificent head of *E. orthostomus* (P. 3633 *b*) in the British Museum figured by Woodward (1895, pl. IV, fig. 1) the horizontal pit-line groove can be observed crossing the lower "suborbital", and its separated anterior part may be seen on the member of the infra-orbital series lying at the postero-ventral margin of the orbit. The groove for the vertical pit-line lies on the lower "suborbital", immediately ventral to the horizontal groove (fig. 8 A). The head, P. 1543 in the British Museum, ascribed to "*Heterolepidotus sauroides*" (=*Eugnathus philpotae* Ag.) Egerton shows the cheek well. Here there are four suborbital plates, and the horizontal pit-line groove may be observed on the second plate from above: it has an anterior continuation on the adjacent post-orbital, and a groove on the pre-opercular indicates its posterior limit. The pit-line was therefore fully developed in this form. The vertical pit-line forms a groove on the next most ventral plate (fig. 8 B).

Amia represents a condition in which the "suborbitals" are greatly reduced and probably occasionally altogether absent, the post-orbital plates having grown very large to cover the cheek. It is worthy of note that the interesting Cretaceous fish *Sinamia* described by Stensiö (1935) has only slightly expanded post-orbitals, and although no "suborbitals" are described by Stensiö (his suborbitals are the bones which most palaeontologists call infra-orbitals) there seems to be remnants of such bones preserved (*loc. cit.* pls. IV, X). In the development of *Amia calva* (Pehrson, 1922, p. 45) it has been found that the post-orbital bones begin as rudiments, associated with sensory organs of the infra-orbital canal, from which lamellae grow backwards and cover most of the cheek. There is only, therefore, a casual relationship between the lower post-orbital and the cheek pit-lines which it comes to underlie, though the pit-lines leave grooves on the surface of the bone (fig. 8 C). It should be mentioned here that Stensiö believes the Amiids to be derived from the Eotriassic Ospiids, which are either closely allied to or members of the family Parasemionotidae Piveteau; at present the evidence seems insufficient for a definite pronouncement.

A third great group of Mesozoic "ganoids" seems to lead up towards the Teleosts: of these *Pholidophorus* and *Leptolepis* are among the best preserved. In this group the "suborbitals" are reduced or absent, and the post-orbitals are enlarged to a greater or less degree. The conditions are rather like those

in *Amia*, therefore, and it is not surprising to find, in a few specimens of *Pholidophorus* from the Lower Lias of Lyme Regis, that the cheek pit-lines form grooves on the lower postorbital, the furrow for the horizontal pit-line extending also on to the pre-opercular (fig. 8 D).

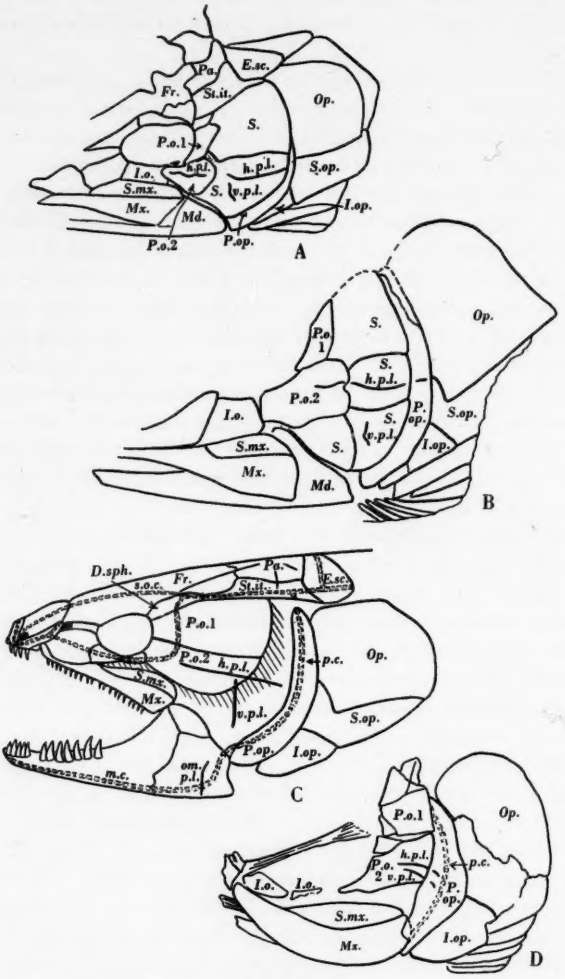

Fig. 8. A. Cheek of *Eugnathus orthostomus* Ag. From specimen P. 3633 *b*, B.M.N.H. Lower Lias, Lyme Regis. B. Cheek of "*Heterolepidotus sauroides*" (=*Eugnathus philpotae* Ag.). From specimen P. 1543, B.M.N.H. C. Cheek of *Amia*. Derived from Allis. D. Cheek of *Pholidophorus* sp. Specimen P. 267, Palaeontology Collection, Department Zoology, University College, London.

TELEOSTEI

The group of Mesozoic "ganoids" in which the "suborbitals" are reduced or absent (e.g. *Pholidophorus*) have a cheek closely resembling that of any ordinary Teleost fish, in that there is a gap between the circumorbitals and the pre-opercular. This gap is sometimes masked in Teleosts by the exuberant growth of circumorbital bones associated with the infra-orbital sensory canal (as in the mail-cheeked Fishes). The dermal bones in Teleostei have, in general, come to have a much closer connection with the "primordial" skull than in earlier bony Fishes, and this has apparently led to the ossification as a whole taking place far below the epithelium. The gradual depression of the level of ossification has frequently caused the separation, partial or complete, of small components still related to sensory canals. The writer regards this as due to the secondarily developed importance of dermal bones in skull architecture and mechanics, rather than showing the existence *ab initio* of different "components" of the dermal bones as suggested by Allis (1935, etc.).

The horizontal and vertical cheek-lines have been described in a number of Teleosts, but they never, so far as the writer is aware, leave any surface marks on the bones. They may, of course, overlie some members of the post-orbital series, but it is quite certain that such connection is casual, as in *Amia*. The structure of the cheek of Teleosts presents one other point of immediate interest; that is the nature of the supramaxillaries. These bones first appear in the Triassic Parasemionotidae, but do not occur in Semionotidae: they are known in Eugnathids, Pachycormids and other groups of Mesozoic ganoids and are usual in Teleosts. The problem of their origin is hardly capable of being settled with our present knowledge of the Mesozoic Fishes: but it seems rather probable that one of the two following hypotheses will be found to be correct: (i) the supramaxillaries may represent new formations, or (ii) they may be remnants of the "suborbital" series.

GENERAL DISCUSSION

In all the primitive members of the great groups of bony fishes (all early Crossopterygii, Dipnoi, and Actinopterygii) and in Ichthyostegalia (Säve-Söderbergh, 1932), the sensory canal system is largely enclosed within the bones, the principal exceptions being the anterior, middle and posterior pit-lines of the skull roof, the vertical pit-line of the cheek and the horizontal and vertical mandibular pit-lines.

In the group of *Choanata* (as defined by Säve-Söderbergh, 1933, p. 118) the jugal canal is enclosed in the dermal bones in all Rhipidistia, all Coelacanths, at least most Dipnoi, and the Ichthyostegalia. The typical condition is that found in *Osteolepis* and *Ichthyostega*: the cheek is here formed by three dermal bones, the squamosal, pre-opercular and quadratojugal. In the Tetrapods, the dermal bones quickly cease to enclose the sensory canals and the

pre-opercular is lost in the cheek. In the Rhipidistia the only modification of importance is the subdivision of the squamosal and the addition of small dermal bones in *Holoptychius*, a change almost certainly due to the elongation of the cheek to provide a more oblique suspensorium and a wider gape. The Coelacanths have undergone important changes connected with the loss of the maxillary: it seems very probable that the quadratojugal has disappeared. Small scale-bones appear behind the pre-opercular, which possibly belong to the opercular fold. Finally in *Axelia* there seems to have been very considerable reduction in this region.

The Dipnoi have adopted a crushing dentition, and have attained an almost vertical suspensorium even in the Middle O.R.S., obtaining thus a better mechanical advantage. In consequence the cheek region has been compressed between the opercular apparatus and the orbit: yet representatives of squamosal, pre-opercular and quadratojugal can be recognised in *Dipterus* and *Scaumenacia*: in other fossil Dipnoi this region is not as a rule preserved, but slight traces of bones connected with the jugal and pre-opercular canals are still to be found in the recent *Neoceratodus*.

It is not easy with our present knowledge to assess the nature of the relationship between the Crossopterygii and Actinopterygii, although the transverse division of the cranium in the former has sufficed for long to mask the real homologies of the dermal bones even between Crossopterygii, Dipnoi and Tetrapods (author's unpublished work). It seems likely to the writer that the two groups diverged from a common ancestor not long before the Devonian. The structure of the cheek in the two groups is one of the most important differences. In the Actinopterygians there is no trace of the large Osteolepid squamosal, and the jugal canal has disappeared as a closed canal, being represented by the horizontal cheek-line of pit-organs: on the other hand, the pre-opercular canal and bone have extended dorsally over the region occupied by the spiracular cleft in Rhipidistia. In *Cheirolepis* there is a possible remnant of the quadratojugal, not found in any later members of the group if we except the very doubtful scale-bones (probably neomorphs) in *Polypterus*.[1]

In order fully to appreciate the problem of the fate of the squamosal in Actinopterygians it will be necessary to digress for a while. There is now a considerable body of evidence in favour of the view that many of the dermal bones of the skull in primitive bony Fishes are in some way rather intimately connected with the sensory canals during development. Pehrson's work on *Amia* (1922) remains one of the most important pieces of evidence from the developmental side, but the examination of large numbers of primitive fossil Fishes, checked by certain embryological observations, has assured the writer that there is very strong support for the theory. It remains for future investigation to show how far the conditions found in many Teleosts are secondary and due to the tendency for the dermal bones of the latter to sink beneath the epidermis and become firmly fixed to or incorporated into the endocranium,

[1] But see postscriptum! (p. 382).

or to take on important functions not found in primitive Fishes. The writer has found the following a useful, suggestive and dependable working hypothesis: that in primitive bony Fishes bone rudiments began to form in close relationship with the sensory organs of the larval lateral line, already sunk deep beneath the surface in gutters, closed channels or in deep pits connected by grooves. The bone was quite probably passive in its method of origin, depending on the physico-chemical conditions set up by the sensory organs being thrust into the underlying mesenchyme and not on any special trophicity for sensory organs or nerve endings. Whatever the cause the writer regards it as highly probable that *such an ossification rudiment was formed*, in general, *in relation to any sensory organ which was sunk in a pit, or to a group of organs in a deep channel or gutter*. From these rudiments, some of which may possibly have fused together, grew the bones traversed by the lateral line in the adult. In addition, several important regions of the head (orbit, possibly pineal body, opercular fold) were protected also by general dermal bones. Moreover, in order to fill up any space and to form a complete "carapace" a mosaic of dermal bones would frequently fill in spaces not already covered by bones mentioned above: for these the writer has elsewhere proposed the descriptive term *anamestic* (Westoll, 1936, p. 166). (It is hardly proper to treat here of the origin of tooth-bearing bones, as the literature on this subject is enormous: but it has been observed (e.g. Moy-Thomas, 1934, and author's observations) that teeth may be formed independently of the bone on which they will later be fixed: and the writer has suggested (*op. cit.*) that the teeth may just become attached to whatever bone is near, whether of lateral line or general dermal origin: hence the tooth-bearing bones have not been specially discussed above, although it is usual to consider a separate class of "tooth-bearing bones".)

During the history of the bony Fishes, several sensory canals have undergone a process of "regression" to the state of a pit-line, in which the organs do not sink beneath the skin. In such a case it is reasonable to suppose, on the working hypothesis outlined above, that the stimulus for bone growth may be gradually removed, and that a bone may thus become small and finally disappear. The dermal cranial roof is of the greatest interest from this point of view, and will be considered on another occasion. It may be pointed out, however, that a bone which has come to have an important protective or functional role may be preserved even though the sensory-canal stimulus for its appearance has been removed.

Let us now apply this to the Actinopterygian cheek. We have seen that the jugal canal of *Choanata* is represented by the horizontal cheek-line of pit-organs, which of course, remains on the surface. Consequently, the bone rudiments associated with the sensory organs of the jugal canal, which form in the adult the squamosal of the Rhipidistia, would not be expected to appear; and in fact we find no trace of a squamosal in the known members of the Actinopterygians. The pit-lines themselves do not imply that the bones on which they are found contain a "squamosal" element: the writer has been

able to show (in *Dipterus*, etc.) that pit-lines may have extremely different courses in different individuals of the same species, and it seems probable that the first bone to grow into the region of a pit-line will be likely to surround the nervous supply of the pit-line, which will thus become "anchored" to the bone in question. In Palaeoniscoids the cheek is mainly covered by the expanded maxillary and pre-opercular: in the more typical members of the group the former is more extensive, and the pit-lines lie on it, but in others (e.g. *Canobius* and *Eurylepis*) the form of the cheek is different and they are associated with the pre-opercular. In many Triassic derivatives of the "Palaeoniscoids" the pre-opercular is large and the pit-line grooves are found on this bone (e.g. *Perleidus*, *Parasemionotus*, etc.). A similar condition is found in *Polypterus*.

In many Mesozoic and later "ganoids" the pre-opercular and maxillary are much reduced, and the "suborbitals" come to occupy much of the cheek, and in some forms the cheek pit-lines are seen to lie on separate members of this series (e.g. *Lepidotus* and *Lepidosteus*). In *Amia* the suborbitals have disappeared except for occasional tiny plates and in *Pholidophorus* these have quite gone, and the cheek is covered by the expanded post-orbitals, the lower one of which comes to underlie the pit-lines. In some Teleosts the expanded post-orbitals cover at least part of the cheek, and often underlie the pit-lines, but in others they are narrow and the cheek between them and the pre-opercular is bare of dermal bones.

CONCLUSIONS

The fate of the cheek-bones in *Choanata* is to a considerable degree connected with differences of feeding habits: in the whole group, however, the squamosal is a characteristic bone, lost only perhaps in some late Dipnoi. In Coelacanths the quadratojugal is lost, while in Tetrapods the pre-opercular has only an ephemeral appearance.

Though it is possible that the Actinopterygii had an ancestor in which there was a squamosal bone connected with a jugal canal, in all the known members of the group the canal has "degenerated" to the horizontal cheek-line of pit-organs, and the squamosal has no existence. The quadratojugal possibly occurs in *Cheirolepis*, and bones in a somewhat similar position in *Polypterus* are probably neomorphs.[1] The pre-opercular and maxillary have large expansions in primitive forms, but first the latter and afterwards the former are reduced, and the "suborbitals", which have probably arisen within the group, become increasingly important. In *Amia* and some Teleosts the "suborbitals" are reduced, and the post-orbitals may be large, covering much of the cheek. Finally in most Teleosts the post-orbitals, the dermal covering of the cheek, are reduced.

Throughout this long process of development the horizontal and vertical

[1] But see postscriptum! (p. 382).

cheek-lines of pit-organs are associated with maxillary, pre-opercular, suborbitals and post-orbitals in turn, and it is an important point that embryological work shows that the connection is casual in at least *Amia calva*: it is fairly certain that the existence of a pit-line groove on a bone, therefore, affords no certain evidence for homology, however valuable the sensory canals proper may be in this respect. Unpublished work on Dipnoi strongly supports this conclusion, and shows that the sensory canals are of very great value in homology.

KEY TO TEXT-FIGURES

Ang.	Angular.	*Qu.j.*	Quadratojugal.
Cor.	Coronoid.	*S.*	"Suborbitals".
D.	Dentary.	*S.ang.*	Supra-angular.
D.sph.	Dermosphenotic.	*S.mx.*	Supramaxillary.
E.sc.	Extrascapular.	*S.o.*	Supra-orbital.
Fr.	Frontal.	*S.op.*	Subopercular.
I.o.	Infra-orbital.	*Sq.*	Squamosal.
I.op.	Interopercular.	*Sq.* 1 and 2.	Separate parts of squamosal.
I.t.	Intertemporal.	*S.t.*	Supratemporal.
Ju.	Jugal.	*St.it.*	Supratemporo-intertemporal.
La.	Lacrimal.	*X* and *Y*	Bones in cheek or opercular series of *Cheirolepis*.
La.ju.	Lacrimo-jugal.		
Md.	Mandible.	*h.p.l.*	Horizontal pit-line of the cheek.
Mx.	Maxillary.	*i.o.c.*	Infra-orbital canal.
N.	Bones in *Polypterus*, probably neomorphs.	*j.c.*	Jugal canal.
		m.c.	Mandibular canal.
Op.	Opercular.	*om.p.l.*	Oralo-mandibular pit-line.
Pa.	Parietal.	*p.c.*	Pre-opercular canal.
P.o.	Post-orbitals.	*s.o.c.*	Supra-orbital canal.
P.op.	Pre-opercular.	*v.p.l.*	Vertical pit-line of the cheek.
P.op. 1 and 2.	Separate parts of the pre-opercular.		

All the figures are redrawn or original, and have been arranged facing the same way to give uniformity of style. For any errors and alterations the writer takes full responsibility.

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POSTSCRIPTUM. (22*nd May*, 1936.)

Since writing this paper, the writer has, during a recent visit to Stockholm, been shown a number of Palæoniscids (mostly from the Eo-Trias of East Greenland) by Dr Eigil Nielsen. These show, in many cases, a small bone in the position of the quadratojugal of *Cheirolepis*, and Dr Nielsen believes that the bone is associated with the vertical pit-line. This discovery does not affect the general conclusions advanced in the paper, merely showing that the bone in question is retained in the "Palæoniscids" longer than was known. It is possible, however, that it may affect the nomenclature of the cheek-bones in *Saurichthys* (fig. 5A), where the course of the pre-opercular canal is not fully known. Dr Nielsen's discovery is published in *Medd. Grønland*, 1936, Bd. CXII, No. 3, and the writer is greatly indebted to him.

THE OSSIFICATION OF THE HUMAN FRONTAL BONE

WITH SPECIAL REFERENCE TO ITS PRESUMED PRE- AND POST-FRONTAL ELEMENTS

By VERNE T. INMAN, M.D., Ph.D. and JOHN B. de C. M. SAUNDERS, M.B., F.R.C.S. (Edin.)

Division of Anatomy, University of California Medical School

INTRODUCTION

In a recent number of the *Journal of Anatomy* there has appeared an article by Ashley-Montagu on the presumed existence of a post-frontal element in the skull of a young gorilla. Ashley-Montagu's conclusions are based largely on the view that the post-frontal bone is present in the developing skull of probably all primates and certainly of all men. "It is not widely known among anatomists", he says, "that the post-frontal bone is a constant element of the developing human skull. For some extraordinary reason most modern textbooks of anatomy and embryology make no mention of the post-frontal element of the human foetal skull in spite of the fact that a constant and independent centre of ossification of this bone is present in every case, and the bone itself may generally be observed up to the end of the third foetal month, and not rarely in the skulls of newborn children."

Having available a considerable collection of material specifically prepared to demonstrate the ossification of the skull in man, we were prompted to seek for this element. We were surprised, in the light of the above definite statement, that we were unable to find the slightest trace of this element occurring as an independent centre, nor were we at any time able to find such other secondary centres of ossification as have been commonly described for the frontal bone. We noted, furthermore, that there was some disagreement among the authors of various standard textbooks, and it became increasingly apparent that in view of the great morphological and phylogenetic conclusions which have been based upon the supposed existence of such secondary centres, reinvestigation of the ossification of the frontal bone was necessary.

LITERATURE

Gabriel Fallopio appears to have been one of the first to state clearly that the frontal bone constantly develops from two symmetrical halves. In his *Observationes Anatomicae* (1561) he says: "Ita ut in omnibus puerulis qui tenerimi sunt frontis os ex duabus constare partibus reperierim." Vesalius was also well aware of this mode of origin of the frontal bone, for not only does

he discuss Fallopio's observations in his *Observationes Gabrielis Falloppii Examen* (1564), but the matter is mentioned in the *Fabrica* (1543). Jhering states that Galen was ignorant of this fact, but it would seem on examining his *De usu partium* and *De administrationibus anatomicis* that he may have been aware of this in some instances.

Up to the time of Kerckring (1670) but few serious attempts had been made to examine the origin of the bones before birth. This author dissected and described specimens from approximately the second month of foetal life.

Albinus illustrates in his *Icones ossium foetus humani* (1737) that area which has since been called the post-frontal element and records an instance in which each half of the frontal bone was divided into three parts. This single observation was made on an aborted foetus. He says: "In abortu juniore, cui totum os magnitudinis unguis mediocris, utramque illam partem inveni divisam in tres; superiorem, quae ad frontem pertinet; inferiorem, quae ad foramen oculi, tertiam quae ad caput supercilii."

Apart from the single observation quoted above from Albinus, the recognition of secondary or accessory centres of ossification dates from the work of Serres (1829).[1] This author described accessory centres, (1) for the part of the pars orbitalis at the trochlear fossa and (2) for the zygomatic process. Serres considered them, in association with his studies on the comparative anatomy of the skull, as representing the pre- and post-frontal elements. Rambaud & Renault (1864) accept the findings of Serres, but do not appear to have seen these centres as independent ossicles. They state that at the fourth month the centres have already been joined by a suture which leaves only a shallow groove and that the centres have always so appeared at this time. These authors added a third centre for the nasal spine which, they state, appears late, sometime after the eighth year.

A fourth centre, for the posterior part of the pars orbitalis, is given by von Spee (1896) in von Bardeleben's *Handbuch*. The existence of such a centre appears to be based on an observation originally made by Hyrtl (1860) that a Wormian bone is sometimes found in this region. Von Spee also observed such a Wormian bone and accepts Hyrtl's conclusion that this has arisen from an independent centre of ossification. It has frequently been pointed out since (Patten, 1912) that the presence of a Wormian bone cannot be accepted as evidence of a true secondary centre.

Since the publication of Rambaud & Renault's monograph, a number of special papers have appeared on the ossification of the frontal bone and on its pre- and post-frontal elements. Lecourtois (1869) published a study based upon foetal skulls of 5–6 months, in which he expresses agreement with the findings of Serres and of Rambaud & Renault.

[1] Many authors give as references to the work of Serres on accessory centres the *C.R. Acad. Sci.*, Paris, 1819 and 1838. These abstracts contain no mention of specific centres. Rambaud & Renault also give as reference Serres, *Des lois de l'ostéogénie*, Paris, 1829. This work is unavailable to us. It would seem that the majority of authors have quoted Serres through Rambaud & Renault.

In 1872, von Jhering published an important paper which has since been widely quoted. Jhering, after reviewing the work of earlier authors, confirms the conclusions arrived at by Rambaud & Renault. He examined, however, no specimen earlier than the 4th month and at no time saw the assumed accessory centres as independent ossicles. Maggi (1897, 1898) published two extensive articles on the morphology of the cranial and cranio-facial bones in which he concludes that the existence of accessory centres for the frontal bone has been satisfactorily demonstrated, and that two of these centres are homologous with the pre- and post-frontal elements of other forms. His observations on man were based on the examination of foetal skulls from the 5th month and on the work of Rambaud & Renault. Finally von Bardeleben (1896), Augier (1912) and Ashley-Montagu (1931) have written articles which, on analysis, present no original observations on the development of the frontal bone, but whose conclusions are either directly or indirectly based on the acceptance of the work of Serres and of Rambaud & Renault.

It is not surprising in consequence, that the standard textbooks of anatomy and of embryology almost uniformly describe and illustrate, apart from the primary centres, three pairs of accessory centres: (1) for the frontal spine, (2) variously for the medial angular process or trochlear pit (pre-frontal element), and (3) for the region of the zygomatic process (post-frontal element). These accessory centres, apart from that for the frontal spine, are, in the general concensus of opinion, assumed to appear about the 4th month and to fuse at the 7th. The centre for the nasal spine is recognized as appearing late, at or before the 10th year. In addition Quain and von Spee (von Bardeleben's *Handbuch*) mention the occasional occurrence of a fourth pair for the postero-medial part of the orbital plate. The statements in Quain, Cunningham, Gray, Morris, Piersol, Gegenbaur, Merkel, von Bardeleben, Testut, and Poirier, are, as in the special articles noted above, a continuation of the opinion of Serres and of Rambaud & Renault.

The only dissenting opinions which we have been able to find in the literature are those of Toldt and Le Double. Toldt, while recognizing the areas described by Serres and by Rambaud & Renault, is unable to accept these as indicating the existence of accessory centres. In Maschka's *Handbuch d. gerichtlichen Medizin* he says: "Ich habe etwas Derartiges beim Menschen nie gesehen und muss daher die Angaben von Serres, Rambaud u. Renault, welche durch Jhering auch in die deutsche Literatur übergegangen sind, wonach beim Menschen ein ursprünglich selbständiges Os frontale posterius bestehe, in Abrede stellen. Ebenso wenig kann ich für den Menschen die Existenz eines zu irgend einer Zeit isolierten Os frontale anterius einräumen."

Le Double discusses extensively the ontogeny and phylogeny of the pre- and post-frontal elements and points out the lack of agreement among anatomists. The existence of accessory centres in man has arisen, in his opinion, from misinterpretation of the findings.

This survey would indicate that the present belief that accessory centres

for the frontal bone exist in man depends in large measure on the observations and interpretation of Serres and of Rambaud & Renault. In spite of the denial of their existence by Toldt, whose opinion is unfortunately buried in a textbook of forensic medicine, and the questioning of Le Double, all modern textbooks of anatomy continue to illustrate and describe such centres. Furthermore their existence forms the chief basis for their acceptance as pre- and post-frontal elements.

MATERIAL AND METHODS

Our observations are based on a total of ninety-eight specimens ranging from the 6th week of intra-uterine life to the 10th month, post-natal. All the material was Caucasian. The majority of the specimens were prepared to demonstrate ossification by a technique developed in this department. This method is much more satisfactory than that of Schultze in that it enables one to follow the progress of ossification to term. The method, published elsewhere by R. Skarda (1934), briefly consists in the rapid dissection of fresh foetal material which has previously been thoroughly freed from blood by washing via the umbilical vessels. The specimens are then hardened in 95 per cent alcohol for 48 hours and cleared in 1 per cent solution of NaOH and finally permanently mounted in 2 per cent formalin solution. The clearing process is carried out in darkness which improves the development of the final preparation. This technique results in preparations of great beauty. The bone is pure white, and its finest ramifications can be traced with ease when viewed in good light under the dissecting microscope. The cartilage remains opalescent blue in colour. Shrinkage is approximately 2 per cent and distortion negligible. The specimens are mounted intact. This is a great advantage in that relations are maintained and there is little danger of creating artifacts. Furthermore the fact that the specimens are wet avoids cracking of the delicate bone which has given rise to so many of the erroneous observations of earlier workers on ossification.

The above technique demands absolutely fresh material. Foetuses of 6 months or over, if not fresh, tend to be opaque, and the ramifications of the delicate trabeculae cannot be made out with the same clarity. This can be remedied by carrying the preparation a stage further. The less satisfactory material is carefully dehydrated by carrying it successively from 50 per cent to absolute alcohol in steps of 5 degrees and then transferring to pure benzol. Specimens prepared in this second fashion show distinctly more shrinkage, and although the most delicate bone centres can be seen and readily followed, they do not have the same elegance as the others, nor do they have the same permanency.

In addition, dissections were made of formalinized specimens and a few dried foetal skulls examined.

OSSIFICATION OF THE FRONTAL BONE

The primary centres

It is universally agreed that the frontal bone ossifies from two primary centres which appear in membrane between the fortieth and fiftieth day. There is some disagreement however with regard to the precise position in which these centres arise. The majority of investigators and most standard textbooks describe ossification as beginning in the position of the future frontal eminences; the minority place the centres at the superciliary region.

We have observed the frontal bone appearing as two finely reticulated areas of ossification in specimens of 32 and 36 mm. sitting height (S.H.). In these and in all other specimens of approximately the same age ossification involves an area whose long axis corresponds approximately to the position of the superciliary arch, and which forms the lower part of the frontal squame and the more anterior portion of the orbital plate and a primitive medial angular process. In our younger specimens this ossific centre is about 2 by 3 mm. The ossific meshwork is of regular and even density throughout this area except for a slight thickening and condensation which forms a line in the position of the primitive supraorbital margin. In slightly older specimens a few fine, less dense trabeculae project radially from the periphery of the centre. These trabeculae are best defined along the upper margin of the developing pars frontalis.

After the appearance of the primary centres, ossification spreads more rapidly in the pars frontalis than in the pars orbitalis. Ossification proceeds in the pars frontalis by the formation of heavy islands of bone which constitute a crescentic area whose maximum depth corresponds to the future postero-superior angle (see Pl. I, fig. 1). These islands fuse to form a series of primary radiating trabeculae (Pl. I, fig. 2). The appearance of secondary trabeculae serves to link the primary trabeculae, expanding the even meshwork of the primary centre. This expansion of the meshwork of the primary centre behind the advancing zone of ossification gives rise to the appearance of a centre in the position of the frontal eminence from which the primary trabeculae radiate, an effect which is often seen in specimens of 4 months and older. In fact, however, this false centre of radiation rises higher and higher up on the frontal squame with increasing age.

In the pars orbitalis the progress of ossification is less rapid. The radiating trabeculae so characteristic of the pars frontalis are very much smaller and less obvious and an expanding meshwork of trabeculae is maintained.

These observations show that ossification begins in the region of the superciliary arch and simultaneously gives rise to a portion of both the pars frontalis and the pars orbitalis and to the primitive medial angular process. The common statement that ossification commences at the site of the future frontal eminence is erroneous, and is undoubtedly the outcome of observations made on older specimens.

The secondary centres

In the ninety-eight specimens examined we have at no time been able to find any true accessory centres of ossification. No centres appear in those regions in which they have been stated to occur. In all instances the bony trabeculae were found to be continuous and unbroken. Furthermore, the regions in which such accessory centres are presumed to arise do not correspond to those in which secondary island formation is found. The specimens on which we base our observations are of such clarity that there is little possibility that such centres, had they existed, could have been overlooked. None the less, if dried preparations of foetal skulls between the third and seventh months, and in some at term, are examined, there are appearances which suggest the possible existence of secondary centres. It is these appearances which have, no doubt, been accepted by many authors as indicating the existence of accessory centres. We shall therefore consider the changes which occur in those areas which have given rise to error in interpretation.

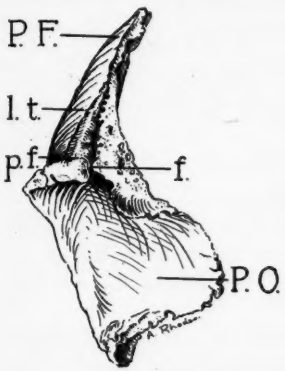
(1) *The presumed centre for the zygomatic process or post-frontal element.*

The primary centre of ossification gives rise to a part of the frontal and orbital plates and a primitive medial angular process. The bony superior orbital margin seen at this period does not correspond to that of the adult. The lateral two-thirds from the position of the future supra-orbital notch to the zygomatic process is due to an entirely new formation. At 42 mm. S.H. a linear thickening of osseous material appears in the lateral two-thirds of the orbital margin at the junction between the pars orbitalis and pars frontalis. This thickening becomes more and more apparent as it is followed laterally, and has resulted in the formation at birth of almost the entire supero-lateral wall of the orbit as well as giving rise to the zygomatic process, and thereby completes the separation of the orbital cavity from the temporal fossa. At 49 mm. S.H. it has spread to form a recognizable zygomatic process which is more apparent at 59 mm. S.H. (see Pl. I, fig. 2). A considerable interval exists between this process and the frontal process of the zygomatic bone; an interval which persists until the foetus has attained a length of 250 mm. The closure of this interval is due to a further extension of ossification in the frontal process of the zygomatic bone rather than to any further ossification in the zygomatic process of the frontal, for at 155 mm. S.H. the proportions of the zygomatic process of the frontal have almost attained those seen at birth.

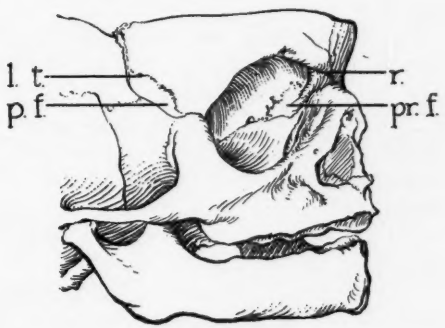
From 49 mm. S.H. onwards the base of the zygomatic process of the frontal, including the lateral two-thirds of the orbital margin, progressively thickens. This thickening extends dorsally on to the lateral surface of the pars frontalis but does not involve its postero-lateral angle. This angle is, as a result of this thickening, bounded antero-superiorly by a ridge. The ridge and the area bounded by it becomes, with further growth of the skull, more and more apparent until, in any specimen from the third month on, a pseudo-suture

appears to separate off this angle, giving rise to the appearance of an autonomous centre. In a macerated skull at 7 months, the ridge extends upwards and dorsally from the posterior border of the zygomatic process (lateral angular process) to a point some 5 mm. above the pterion (Text-fig. 2, *l.t.*). This ridge delimits a quadrilateral area of bone, approximately 5 mm. in height and 15 mm. in length, which includes the postero-lateral angle (Text-fig. 2, *p.f.*). Dissections and histological sections demonstrate that this ridge gives attachment to the temporal muscle and is none other than the linea temporalis. This is confirmed by the finding, in a few specimens, of a continuation of the ridge on to the antero-inferior angle of the parietal bone.

In the disarticulated frontal bone, the new process which springs from the margin between the pars frontalis and orbitalis, and which completes the



Text-fig. 1.



Text-fig. 2.

Text-fig. 1. Postero-inferior view of the left disarticulated frontal bone of 7 months' old human foetus. *P.F.* pars frontalis; *P.O.* pars orbitalis; *l.t.* linea temporalis; *p.f.* "presumed" post-frontal element; *f.* superior limb of fissure separating supero-lateral process from the pars orbitalis.

Text-fig. 2. Lateral view of the facial region of a full-term human foetal skull. *p.f.* "presumed" post-frontal element; *l.t.* linea temporalis; *pr.f.* "presumed" pre-frontal element; *r.* ridge separating the medial angular process from the pars frontalis.

supero-lateral wall of the orbit and gives rise to the zygomatic process, is separated postero-laterally, from the rest of the pars orbitalis, by a deep fissure (Text-fig. 1, *f.*). This fissure gives attachment to the membrane filling the lateral fontanelle. The inferior limb of the fissure extends on to the roof of the orbital cavity, in the floor of the lachrymal fossa. The inferior limb of the fissure is obliterated, medio-laterally, at birth, but usually persists as a linear series of small foramina and is often evident in the adult. The presence of this fissure in the later months of intra-uterine life further falsely accentuates the appearance of an independent centre of ossification in this area.

The area outlined by the linea temporalis and the fissure described above constitutes what has been designated as the post-frontal element of the human

frontal bone, and has been regarded as arising from an autonomous secondary centre of ossification.

(2) *The presumed centre for the medial angular process (trochlear pit) or pre-frontal element.*

A primitive medial angular process is ossified simultaneously with the appearance of the primary ossific centre. This process appears to be a continuation of the superciliary margin medially and forms a small portion of the anterior part of the medial wall of the orbit. At 49 mm. S.H. only the more anterior portion of the pars orbitalis is osseous. At this time ossification is relatively more extensive in the medial angular process.

Ossification spreads much more slowly in the orbital roof and in consequence an unossified interval persists, until the 4th month, between that part of the medial angular process which lies in the medial wall of the orbit and the roof.

At 59 mm. S.H. the medial angular process commences to show some thickening of its reticular network, whereas at this time scarcely a third of the orbital plate is ossified.

At 80 mm. S.H. ossification has spread to complete the major part of the orbital plate and it commences to fuse with the medial angular process, obliterating the interval between these structures. This line of fusion is indicated at birth either by a groove, or by a series of foramina resembling a suture, which runs obliquely across the trochlear pit to the anterior end of the fronto-ethmoidal suture (Text-fig. 2).

At 59 mm. S.H. a slight thickening extends medially from the position of the future supra-orbital notch across the base of the medial angular process to the metopic suture (Pl. I, fig. 2). This thickening indicates for the first time the boundary of the permanent orbital rim. At 99 mm. S.H. the trabeculae have thickened to such an extent as to produce a ridge which separates the medial angular process from the pars frontalis, a ridge which is very apparent at term (Text-fig. 2, *r.*). As a result, the superior orbital margin of the foetus is well defined medially. A new margin is therefore formed anterior to the primitive margin which, if traced downwards, becomes continuous with the crista lacrimalis anterior. Between these two margins lies the fossa sacci lacrimalis and the lacrimal sac.

In the later months of foetal life a quadrilateral area of bone is defined in the trochlear region of the macerated frontal bone. This area is bounded anteriorly by the ridge of bone which crosses the base of the medial angular process, superiorly by a groove or series of foramina, inferiorly by the fronto-maxillary, fronto-lacrimal and anterior part of the fronto-ethmoidal sutures (Text-fig. 2, *pr.f.*). Its surface is rough and irregular. It is this area which has been almost universally regarded as the accessory centre for the trochlear pit or medial angular process and which has been designated as the pre-frontal element of man.

The centre for the nasal spine

At no time prior to birth have we ever observed the presence of a secondary centre for the nasal spine. This process remains unossified for some time after birth. Whether the spine ossifies from secondary centres at or about the 12th year, as is usually stated, or whether it ossifies as an extension from the frontal bone, we are not in a position to say.

Radiograms, both flat plates and stereograms, of children up to the age of puberty, have yielded little information. We have seen the nasal spine in both male and female subject at 10 years, when it appears, so far as we can tell, to be in continuity with the rest of the frontal bone. Earlier than this we have been unable to make out the process and have not seen it as a separate centre.

Centre for the posterior part of the orbital plate

As already mentioned, the orbital plate is ossified in the anterior third of its extent simultaneously with the appearance of the frontal centre. The further spread of ossification to complete the formation of this plate is delayed for some time, excepting that part which abuts against the future cribiform plate. At 78 mm. S.H. ossification of the pars orbitalis is almost complete, but for a short time an inconspicuous incisura exists between the main lateral portion of this plate and the earlier formed medial part. These soon fuse. As at the periphery of the superior angle of the pars frontalis, a few islands of osseous material may precede the formation of the reticulum. None of these can be regarded as a true secondary centre, but their independent development may give rise to a Wormian bone such as that described by von Spee. The manner in which ossification proceeds in the pars orbitalis, with the production for a time of an incisura, might give rise, unless carefully followed in many specimens, to the appearance of what we must call a pseudo-centre.

DISCUSSION

It is perfectly apparent that the conception of the development and ossification of the frontal bone found in almost all modern textbooks is fundamentally a repetition of the views originally expressed by Serres, and by Rambaud & Renault, which have been widely disseminated by Jhering's publication. The illustrations which continue to promulgate these misconceptions appear to be, for the most part, based upon those which accompany the treatise of Rambaud & Renault. The observations of Toldt and the opinion of Le Double seem to have had no influence on, and to have affected in no way, the classical description.

It is universally recognized that the frontal bone ossifies from two primary centres. Mall gives the 56th day as the time of their appearance, a little later than that given by Toldt. Our findings are essentially in agreement with those of Mall. The statement that the primary centre of ossification appears at the position of the future frontal eminence is, although exceedingly common,

incorrect. Almost all original observers recognize that ossification commences in the superciliary region, forming simultaneously part of the frontal squame and orbital plate.

We have been unable to find any evidence, at any time in the prenatal period, of true accessory centres of ossification for the frontal bone.

It has been stated that a secondary centre appears in the region of the zygomatic process or in the neighbourhood of the pterion. This centre is regarded by many observers as representing the post-frontal bone of pre-mammalian skulls. We have shown that there is no such centre. What has been accepted as such is an area ossified by extension from the primary centre and modified by the development of the lateral two-thirds of the orbital margin and bounded externally by the temporal line, and internally by a fissure or series of foramina. This fissure extends on to the roof of the orbit and lies in the floor of the lacrimal fossa. It may persist as a series of more or less extensive foramina which occur in the region where the cribra orbitalia of Welcker (1887) are most commonly found. While Welcker denies that cribra are to be found in the newborn, he finds them in the skulls of young children. Both Ahrens (1905) and Koganei (1912) state that they are found most frequently in the young.

We have noted in young skulls with weakly developed cribra that the cribra lie in the precise region of the fissure and we suggest that there is some relationship between the development of the cribra and the blood vessels which enter this region, as has been demonstrated for the cribra cranii.

The lateral two-thirds of the permanent supra-orbital margin arise, as detailed above, as a separate process which serves to close the orbit from the temporal fossa. It also completes the fossa lacrimalis and, appearing late, is not completely fused with the rest of the bone until after birth.

This process leads to the formation in the adult skull of what has been described by Schwalbe (1906) as the planum or trigonum supra-orbitale. An oblique groove separating the trigonum supra-orbitale from the rest of the frontal bone is chiefly characteristic of recent man and occurs in some individuals of all primates. This groove extends from the supra-orbital notch upwards and laterally towards the temporal ridge, and has been named the sulcus supra-orbitalis.

In those forms such as the gorilla, chimpanzee, and the Neanderthal race in which the various supra-orbital elements are blended to form a distinctive torus supra-orbitalis, the sulcus supra-orbitalis may be obliterated, but when found is regarded by Cunningham (1908) as a juvenile character. Although the sulcus is most frequently related to the supra-orbital notch and may contain a branch of the supra-orbital nerve in part or in its entire extent, it cannot in any way be regarded primarily as a nerve pathway.

It has not been recognized that the sulcus supra-orbitalis defines developmentally the level of the primitive orbital margin and that variations in the dimensions of the orbital rim are dependent upon the degree of development of the supero-lateral process.

In the hypertelerotic skull described by Greig (1924), under-development of this process has given to the orbital cavity an exaggerated lateral inclination, and suppression of its medial half has profoundly modified the orbital margin which is megaseme. Greig has pointed out that in hypertelorism there is retention of many foetal characteristics and among them we note retention of the primitive supra-orbital margin.

A study of the development of the eyebrow region and of the supra-orbital margin indicates that the essential primordia in man and the primates are identical. The differences which exist between adult forms are the outcome of differences in developmental direction alone.

We have demonstrated that there is no accessory centre for the medial angular process or trochlear pit and we have described the area which has been erroneously considered as the pre-frontal element.

Opinions differ as to whether the anterior or posterior lacrimal crest should be considered as forming, for purposes of mensuration, the exact medial margin of the orbit. Some have given the posterior crest as the true limit of the orbital contents on the ground that it gives attachment to the septum orbitale. Others have taken the anterior crest. It would appear that the crista lacrimalis posterior is a continuation of the primitive orbital margin on the medial side. The lacrimal sac is therefore at first an extra-orbital structure and only with the formation of the new rim margin does it become potentially intra-orbital. This change in relationship is of ontological and phylogenetic interest. Flower (1907) has shown that in most mammals and of the primates in the lemur alone, the lacrimal fossa is extra-orbital. In all other primates the sac is considered to lie within the orbit.

SUMMARY

1. An historical review of the literature on the ossification of the frontal bone and its accessory centres is given.

2. Observations were made upon a total of ninety-eight foetal skulls ranging in age from the 6th week of intrauterine life to the 10th month postnatal.

3. Primary centres of the frontal bone make their appearance in the superciliary region and the details of ossifications are given.

4. No secondary centres of ossifications have been found at any time in the frontal bone. The changes which have given rise to the error that such centres exist are considered.

5. Attempts which have been made to homologize portions of the frontal bone with the pre- and post-frontal elements of premammalian skulls have been based upon the presumed existence of secondary centres. As no such centres exist in the human skull, such conclusions as have been made, on this basis, must be discarded.

6. The significance of the trigonum supra-orbitalis of Schwalbe and of the sulcus supra-orbitalis as well as of other details about the orbit are discussed.

In conclusion it is with great pleasure we acknowledge our indebtedness to Mrs L. G. Philippe for secretarial assistance, and to Mr Rudolph Skarda for his skill in the preparation of material

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EXPLANATION OF PLATE I

Fig. 1. Untouched photograph (infra-red, Wratten filter No. 25) of norma lateralis of an ossifying human foetal skull, sitting height 80 mm. (13·5 weeks, Streeter's tables).

Fig. 2. Untouched photograph (infra-red, Wratten filter No. 25) of norma facialis of an ossifying human foetal skull, sitting height 126 mm. (16·5 weeks, Streeter's tables).

Fig. 2.

Fig. 1.

UNIV. OF MICH.

THE INTEROSSEOUS MUSCLES OF THE HAND

By C. R. SALSBURY, M.D., C.M.

From the Department of Anatomy, Queen's University, Kingston, Canada

THE writer of this article, both as an industrial surgeon and as a teacher of anatomy, has been greatly interested in the tendons of the fingers. The actual mechanism of flexion and extension of the middle and distal phalanges has never seemed sufficiently clear to explain all clinical observations and considerable thought and work have been devoted to the subject. One cannot go deeply into the physiology of finger movement without coming to the question, "What, exactly, are the function and action of the interossei?" To answer this, one must know their insertions. At this point, one looks to the textbooks in vain.

Brash (1931) states that the palmar interossei are inserted "into the capsule of the metacarpophalangeal articulation, the side of the base of the first phalanx of the finger and into the dorsal expansion of the extensor tendon", and the dorsal "exactly like the tendon of a volar muscle, into the dorsal aspect of each of the four fingers".

According to Lewis (1930), the dorsal interossei "are inserted into the bases of the first phalanges and into the aponeuroses of the tendons of the extensor digitorum communis", while the palmar group are "inserted into the side of the base of the first phalanx and aponeurotic expansion of the extensor communis tendon to the same finger".

Both of the authors, quoted above, give the usually accepted actions; flexion of the metacarpophalangeal joints and extension of the interphalangeal, with the additional action of adduction for the palmar and abduction for the dorsal group.

A little thought will show that the above descriptions of insertion and action are quite inconsistent. A tendon inserting into the proximal phalanx cannot possibly move either of the other phalanges independently of the proximal one, no matter how clearly defined the anatomical attachment to the extensor expansion. Hence, if an interosseous muscle be inserted into the proximal phalanx, it cannot act as an extensor of the middle phalanx on the proximal, nor of the distal on the middle.

Although only two texts were quoted above, the same error, or omission, occurs in the others. Bardeen (1933), it is true, adds the statement that the dorsal interossei have more attachment to the proximal phalanges than have the palmar, and that the lateral ones have more than the medial ones. These facts have been thoroughly substantiated in the investigation to be presently described, but they do not assist in the solution of the insertion-action paradox. Even Wood Jones (1920), in his excellent monograph, does not mention this phase of the problem.

Clearly, then, there must be some fallacy of description and it is possible, even on theory alone, to indicate some of the directions in which it must lie. For any interosseous muscle, one or more of the following must be true:

(1) It may insert wholly into the proximal phalanx.

(2) It may insert wholly into the extensor expansion.

(3) If a single tendon inserts into both the proximal phalanx and the extensor expansion, the insertion into the expansion must be functionally useless and that particular muscle is not an extensor of the interphalangeal joints.

(4) If an interosseous muscle, inserting into both the proximal phalanx and the extensor expansion, is able to exert an independent action on the two, then that muscle must have two separate tendons of insertion, activated by two separate fleshy bellies.

In the above argument, action on the proximal phalanx is considered only as that due to direct insertion into it. This bone must, of course, be subject to the indirect influence of the interosseous insertion into the extensor expansion.

In an attempt to shed some light into this dark corner of anatomy and as a part of the major problem of the extensor mechanism, an investigation of the interossei was undertaken. Both hands of fifteen subjects were carefully dissected and the findings recorded. These hands had been partially used by students and, in some cases, it was impossible to be quite certain of a muscle. All such doubtful muscles were omitted and are represented, in the table below, by a blank space. By coincidence, two specimens of each muscle were unsatisfactory and, although thirty hands were examined, only twenty-eight examples of each muscle were accepted.

Since we were interested in function as well as in structure, an attempt was made to ascertain the possible actions of each muscle. These are recorded as to whether or not they were capable of extension of the interphalangeal joints. It is admitted that every interosseous muscle is able to act on the proximal phalanx, even in the complete absence of any direct attachment to it.

The following symbols are used in Table I:

P. represents the palmar portion of a muscle.

D. represents the dorsal portion of a muscle.

* able to extend the interphalangeal joints.

— not able to extend the interphalangeal joints.

*? action uncertain but probably *.

—? action uncertain but probably —.

? quite unable to decide whether * or —.

It should be remembered that these were embalmed specimens and, although relatively little formalin had been used, this introduces a possibility of error. Any such error, however, must be toward — and away from *.

The classification of the palmar interossei used here is that which accepts

only three. The slip in association with the thumb is not considered, since there is no question of its action.

Table I

Palmar interossei

Body	Side	First	Second	Third
1	R.	Exp. 100 % *	Exp. 100 % *	Exp. 100 % *
	L.	Exp. 100 % *	Exp. 100 % *	Exp. 100 % *
2	R.	Exp. 100 % *	Exp. 100 % *	Exp. 100 % *
	L.	Exp. 100 % *	Exp. 100 % *	
3	R.	Exp. 100 % *?	Exp. 100 % *	Exp. 100 % *
	L.	Exp. 100 % *	Exp. 100 % *	Exp. 100 % *
4	R.	Exp. 100 % *	Exp. 100 % *	Exp. 100 % *
	L.	Exp. 100 % *	Exp. 100 % *	75 % to exp. * 25 % from deep surface to proximal phalanx
5	R.	Exp. 100 % *	Exp. 100 % *	Exp. 100 % *?
	L.	Exp. 100 % *	Exp. 100 % *	Exp. 100 % *
6	R.	D. 30 % bone — P. 70 % exp. *	Exp. 100 % *	
	L.	Exp. 100 % *	Exp. 100 % *	Exp. 100 % *
7	R.	Exp. 100 % *	Exp. 100 % *	Exp. 100 % *
	L.	Exp. 100 % *	Exp. 100 % *?	Exp. 100 % *
8	R.	Exp. 100 % *	Exp. 100 % *	Exp. 100 % *
	L.	Exp. 100 % *	Exp. 100 % *	Exp. 100 % *
9	R.	Exp. 100 % *	Exp. 100 % *	Exp. 100 % *
	L.	Exp. 100 % *	Exp. 100 % *	Exp. 100 % *
10	R.	Exp. 100 % *	Exp. 100 % *?	Bone 100 % —
	L.	Exp. 100 % *	Exp. 100 % *	Exp. 100 % *
11	R.	Exp. 100 % *		Bone 100 % —
	L.	Exp. 100 % *	Exp. 100 % *	Deep 70 % to bone — Sup. 30 % to exp. —
12	R.	Exp. 100 % *	Exp. 100 % *	Exp. 100 % *
	L.		Exp. 100 % *	Exp. 100 % *
13	R.		Exp. 100 % *	Exp. 100 % *
	L.	Exp. 100 % *		Exp. 100 % *

Table I (*continued*)

Body	Side	First	Second	Third
14	R.	Exp. 100 % *	Exp. 100 % *	Exp. 100 % *
	L.	Exp. 100 % *	Exp. 100 % *	Exp. 100 % *
15	R.	Exp. 100 % *	Exp. 100 % *	Exp. 100 % *
	L.	Exp. 100 % *	Exp. 100 % *	Exp. 100 % *

Dorsal interossei

Body	Side	First	Second	Third	Fourth
1	R.	Bone 100 % —	D. 60 % bone — P. 40 % exp. *	Exp. 100 % *	D. 70 % bone — P. 30 % exp. *
	L.	Bone 100 % —	D. 70 % bone — P. 30 % exp. *	Exp. 100 % *	Exp. 100 % *
2	R.	Bone 100 % —	D. 50 % bone — P. 50 % exp. *	Exp. 100 % *	D. 50 % bone — P. 50 % exp. *
	L.	Bone 100 % —	D. 60 % bone — P. 40 % exp. *	Exp. 100 % *	D. 10 % exp. } P. 10 % exp. } * 80 % bone —
3	R.	Bone 100 % —	D. 80 % bone — P. 20 % exp. —?	Exp. 100 % *?	D. 50 % exp. — P. 50 % exp. *?
	L.	Bone 100 %	D. 70 % bone — P. 30 % exp. *	D. 15 % bone — P. 85 % exp. *?	D. 60 % exp. * P. 40 % bone —
4	R.		D. 50 % bone — P. 50 % exp. *	Exp. 100 % *?	D. 60 % bone — P. 40 % exp. *?
	L.	Bone 100 % —	Bone 100 % —	D. 70 % bone — P. 30 % exp. *	D. 60 % bone — P. 40 % exp. *
5	R.	Bone 100 % —	Exp. 100 % *	Exp. 100 % *	D. 60 % bone — P. 40 % exp. *
	L.	Bone 100 % —	D. 75 % bone — P. 25 % exp. —	D. 50 % bone — P. 50 % exp. ?	D. 75 % bone — P. 25 % exp. *
6	R.	Bone 100 % —	D. 50 % bone — P. 50 % exp. *	Exp. 100 % *	Exp. 100 % *
	L.	Bone 100 % —			D. 50 % bone — P. 50 % exp. *
	R.	Bone 100 % —	D. 70 % bone — P. 30 % exp. *	Exp. 100 % *	D. 50 % bone — P. 50 % exp. *

Table I (*continued*)

Body	Side	First	Second	Third	Fourth
7	L.	Bone 100 %	D. 20 % bone	Exp. 100 %	Exp. 100 %
		—	—	*	—
			P. 80 % exp.		
			*		
8	R.	Bone 100 %	D. 70 % bone	Exp. 100 %	Exp. 100 %
		—	—	*	*
			P. 30 % exp.		
			*		
	L.	Bone 100 %	D. 70 % bone	Exp. 100 %	Exp. 100 %
		—	—	*	*
			P. 30 % exp.		
			*		
9	R.	Bone 100 %	D. 50 % bone	Exp. 100 %	
		—	—	*	
			P. 50 % exp.		
			*		
	L.	Bone 100 %	Exp. 100 %	Exp. 100 %	Exp. 100 %
		—	?	*	*?
10	R.	Bone 100 %	D. 50 % bone	Exp. 100 %	Exp. 100 %
		—	—	?	*?
			P. 50 % exp.		
			—?		
	L.	Bone 100 %	D. 70 % bone	Exp. 100 %	Exp. 100 %
		—	—	*	*
			P. 30 % exp.		
			*		
11	R.	Bone 100 %			D. 50 % bone
		—			—
					P. 50 % exp.
					*
	L.	Bone 100 %	Bone 100 %	D. 50 % bone	D. 30 % bone
		—	—	—	—
				P. 50 % exp.	P. 70 % exp.
				*	*?
12	R.	Bone 100 %	Exp. 100 %	Exp. 100 %	D. 70 % bone
		—	*	*	—
					P. 30 % exp.
					*
	L.	Bone 100 %	Exp. 100 %	Exp. 100 %	D. 60 % bone
		—	*	*	—
					P. 40 % exp.
					*
13	R.		Exp. 100 %	Exp. 100 %	D. 95 % exp.
			*	*	*
					P. 5 % bone
					—
	L.	Bone 100 %	D. 80 % bone	Exp. 100 %	
		—	—	*	
			P. 20 % exp.		
			*		
14	R.	Bone 100 %	D. 50 % bone	D. 10 % bone	Exp. 100 %
		—	—	—	*
			P. 50 % exp.	P. 90 % exp.	
			*	*	
	L.	Bone 100 %	D. 70 % bone	Exp. 100 %	D. 30 % exp.
		—	—	*	*?
			P. 30 % exp.		P. 70 % exp.
			*		*
15	R.	Bone 100 %	D. 80 % bone	Exp. 100 %	Exp. 100 %
		—	—	*	*
			P. 20 % exp.		
			*		
	L.	Bone 100 %	Exp. 100 %	Exp. 100 %	D. 50 % bone
			*	*	—
					P. 50 % exp.
					*

The findings shown in detail in Table I are summarized below.

Table II

28 studied. *Palmar* 1
27 (96·4 per cent) wholly to expansion.
1 (3·6 per cent) to expansion and bone.
Actual amount of tendon going to expansion 98·8 per cent.
Actual amount of tendon going to bone 1·2 per cent.

28 studied. *Palmar* 2
28 (100 per cent) wholly to expansion.

28 studied. *Palmar* 3
24 (85·7 per cent) wholly to expansion.
2 (7·1 per cent) wholly to bone.
2 (7·1 per cent) to expansion and bone.
Actual amount of tendon going to expansion 89·1 per cent.
Actual amount of tendon going to bone 10·9 per cent.

Dorsal 1

In every hand examined the first dorsal interosseous inserted wholly into the proximal phalanx. No insertion into the extensor expansion was found in any case.

28 examined. *Dorsal* 2
2 (7·1 per cent) wholly to bone.
6 (21·4 per cent) wholly to expansion.
20 (71·4 per cent) to bone and expansion.
Actual amount of tendon going to bone 51·6 per cent.
Actual amount of tendon going to expansion 48·4 per cent.

28 examined. *Dorsal* 3
0 wholly to bone.
23 (82·1 per cent) wholly to expansion.
5 (17·9 per cent) to bone and expansion.
Actual amount of tendon going to bone 7 per cent.
Actual amount of tendon going to expansion 93 per cent.

28 examined. *Dorsal* 4
0 wholly to bone.
10 (35·7 per cent) wholly to expansion.
18 (64·3 per cent) to bone and expansion.
Actual amount of tendon going to bone 33·6 per cent.
Actual amount of tendon going to expansion 66·3 per cent.

Note that the insertion into the expansion is listed first in the case of the palmar group, but that into the bone first for the dorsal group. This simplifies references as will be seen later.

A consideration of the summary, as outlined above, brings certain points into prominence:

(1) The palmar interossei have very little insertion into the proximal phalanges.

(2) The dorsal interossei are attached to the proximal phalanges much more extensively than are the palmar.

(3) Dorsal 1 is inserted wholly into the proximal phalanx.

(4) Dorsal 2 and dorsal 4 have a greater insertion into the proximal phalanx than has dorsal 3. The order of the dorsal interossei, arranged according to their insertion into the proximal phalanx, is 1, 2, 4, 3. This order remains the same whether one considers the numerical percentage of tendons having an insertion into the bone or the average amount of the total bony insertion.

(5) Except for the first, there is a wide variation in the individual dorsal interossei of the different hands.

In addition to the above conclusions drawn directly from Tables I and II, several other interesting facts were noted during the course of the dissection.

(1) All those dorsal interossei that attached to both the extensor expansion and the proximal phalanx *and were able to act on both* had two separate insertions.

(2) In the majority of such cases, a palmar tendinous band passed to the expansion while a dorsal fleshy part inserted directly into the base of the proximal phalanx. Occasionally, the palmar part went to the phalanx, the dorsal to the expansion.

(3) With two exceptions, all insertions into the proximal phalanx could function only in abduction or adduction. One was so situated as to be able to act as a flexor, one as an extensor.

(4) In many cases, the deep surface of the tendon of a palmar interosseous, or the palmar tendinous band of a dorsal muscle, was loosely or firmly attached to the surface of the joint capsule.

(5) The adjacent edges of the volar and dorsal parts were sometimes adherent. This, together with the adhesions mentioned in (4), was responsible for the uncertainties regarding action, as shown by "?" in Table I.

(6) Most tendinous insertion into the proximal phalanx was intimately fused with the capsule of the metacarpophalangeal joint.

(7) There is a very prominent and, it seems, a very important part of the deep fascia not specifically mentioned in the text-books. This extends across the dorsum, intimately bound to the extensor tendon, down into the web, and is firmly attached to the interosseous tendon of the two sides. On the side where there is a lumbrical, it ends by fusing with that tendon; where there is no lumbrical, it ends at the corresponding interosseous tendon. This fascia is shown in many illustrations, including Luschka's well-known diagram of

the tendons of the middle finger, but I have never seen it described. Mention is justified, however, because we can easily deduce a definite function for it. In flexion of the metacarpophalangeal joint, this fascial sheet anchors the tendons of the interossei and lumbricals. Without it, extension of the interphalangeal joints would probably be impossible while the metacarpophalangeal joint is flexed. This interpretation of its action is greatly strengthened by the very evident fact that the fibres run transversely. It is interesting to note, also, that this sheet of fascia gives an extensive insertion to the common extensor tendon and is probably the most important factor in preventing its functioning as an extensor of the interphalangeal joints. In view of this functional importance, it would seem advisable to have a name and "Transverse metacarpophalangeal fascia" is suggested.

(8) An interosseous tendon, whether a palmar or the palmar part of a dorsal, is usually flattened and, as it crosses the side of the metacarpophalangeal joint, it lies in a plane approximately at a right angle to that of the palm. Very commonly, there is a well-defined band passing between the palmar edge of the tendon and the side of the capsule. Although strong, it was sufficiently loose to permit free play of the tendon and seldom interfered with its movement, but more frequently restricting the dorsal than the palmar. In fact, it seemed to be most highly developed in association with those tendons that were most definitely extensors of the middle and distal phalanges. The following tabulation shows its frequency in 28 specimens of each muscle:

Palmar 1	Palmar 2	Palmar 3	Dorsal 1	Dorsal 2	Dorsal 3	Dorsal 4
14	7	7	0	0	6	4

This is in marked contrast with the statement of Brash and Jamieson (1935) that "Except for the first palmar, they are all bound to the capsule of a metacarpophalangeal joint".

The exact significance of this attachment is not, at present, clear, but it seems to keep the tendon of the palmar interossei, especially, from slipping dorsally.

The differences in the insertions of the various interossei appear too definite to be of no importance. In a search for the factors underlying them, our first interest centred on the lumbricals. Certain facts suggest that they may have an important influence:

(1) Reference to Table II shows that the insertion of dorsal interossei into the extensor expansion increases in the order dorsal 1, 2, 4, 3. Dorsal 1 and 2 are on the same side as a lumbrical, dorsal 3 and 4 are not. Those interossei located on the same side of the digit as the lumbricals have a greater insertion into the proximal phalanx, and a correspondingly lesser insertion into the expansion, than have those on the side without a lumbrical.

(2) In 88 per cent[1] of cases, the first lumbrical is larger than any other. The first dorsal interosseous inserted wholly into the phalanx in all cases studied.

[1] Personal data, unpublished.

In this series, eight lumbricals had an anomalous insertion. There was no evidence that the anomalies in any way affected the arrangement of the interossei.

Although some evidence might be advanced to support a claim that the position of the lumbricals is the factor responsible for the differences in the attachment of the dorsal interossei, such evidence is not sufficiently convincing. It has been shown that the lumbricals are on the side of the interossei with the greater insertion into the proximal phalanges. May this not be accepted as evidence that the lumbricals do assist in interphalangeal extension, being more highly developed where the dorsal interossei are unable to act on the extensor expansion?

A complete tabulation of the lumbricals of these hands will not be presented in this communication, as it seems better to confine our attention to the interossei. A detailed study of the lumbricals may be offered at some later date.

No attempt to explain the functional or developmental significance of these findings will be made at the present time. Certain collateral investigations have been initiated and, should the results appear of sufficient importance, a supplementary report will be offered.

SUMMARY

A study of the interossei of thirty hands brought out certain points not in agreement with the usual textbook descriptions.

1. The palmar interossei are inserted, with few exceptions, wholly into the extensor expansions.

2. The first dorsal interosseous inserts wholly into the proximal phalanx.

3. The other three of the dorsal group have a variable insertion, more frequently into both extensor expansion and proximal phalanx. As a rule, these two insertions are from functionally separate fleshy portions and this separation may be so complete as to form an extra palmar interosseous.

4. The second dorsal interosseous has a greater insertion into the proximal phalanx than has the fourth, and the fourth has more than the third.

5. Several minor anatomical features are described and an attempt made to correlate structure and function.

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THE SHEATH OF THE RECTUS ABDOMINIS

By ROBERT WALMSLEY

Department of Anatomy, University of Edinburgh

A structure of such complexity as the rectus sheath could not fail to attract the attention of anatomists, and its comparative form, its morphological interpretation, and its possible functional significance have been the subjects of numerous studies. The construction of the sheath in the mammals, in which group alone it may be said properly as a sheath to exist, was soon discovered to vary, and to do so not only from order to order but even among related species. The sheath exists in three main forms: (1) the superficial wall of the sheath is formed by the obliquus externus and the deep wall by the obliquus internus and transversus (*Ornithorhynchus*, most marsupials, Talpidae, *Pteropus*); (2) the superficial wall is formed by the obliquus externus and the obliquus internus and the deep wall by the transversus (rabbit, dog, Insectivora (except Talpidae), gibbon, chimpanzee, gorilla); and (3) the obliquus internus splits into two lamellae, one of which with the obliquus externus forms the superficial wall and one with the transversus the deep wall (cat, pig, horse, ox, sheep,

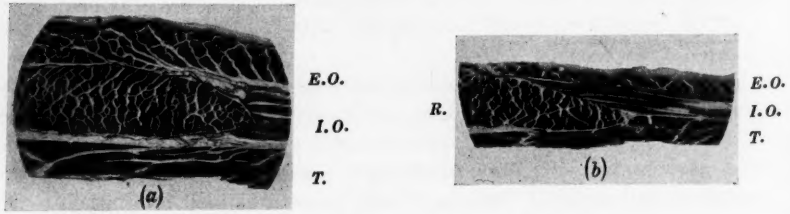

Fig. 1. Transverse sections of the anterior abdominal wall of the mouse; *a*, at the middle part, and *b*, at the lower part.

mouse, man). Further, however, in some species the construction of the sheath is different at its upper, middle, and lower parts, the construction of the middle part being considered to be typical and that of the upper and lower parts to be variants of it. The variations at the upper part are due to the presence of the costal skeleton in the abdominal wall, the primary morphological position of the skeleton being in the middle muscle layer. The variations at the lower part of the sheath have been less satisfactorily explained. They always consist of a shifting forwards into the superficial wall of a part, or the whole, of the deep wall of the sheath, the change taking place in the lower third or lower quarter of the abdominal wall and with an abrupt suddenness so that there is a sharp free border for a part, or the whole, of the deep wall. In the mouse (Fig. 1),

for example, the lower part of the internal oblique muscle, which at the typical level splits to enclose the rectus, suddenly changes its insertion wholly into the superficial wall of the sheath; the transversus alone then forms the deep wall of the sheath as far as its lower border, beyond which the rectus rests on the fascia transversalis. In the dissection of a gibbon it was demonstrated that the transversus, in the lower quarter of its length, suddenly splits into two layers, one of which passes into the superficial wall of the sheath and one continues in the deep wall which it forms as far as the pubis. In the ox and the sheep, as in the human subject, the deep wall of the sheath ceases abruptly in the lower quarter of the abdomen, the lower part of the internal oblique being undivided and with the transversus passing into the superficial wall of the sheath; in the chimpanzee, on the contrary, the transversus maintains its position in the deep wall of the sheath in its whole extent. In a baboon it was demonstrated that the internal oblique passed wholly anterior to the rectus; the deep wall of the sheath was formed by transversus, but midway between the umbilicus and pubis it abruptly passed into the superficial wall, a typical arcuate line (linea semicircularis) being formed.

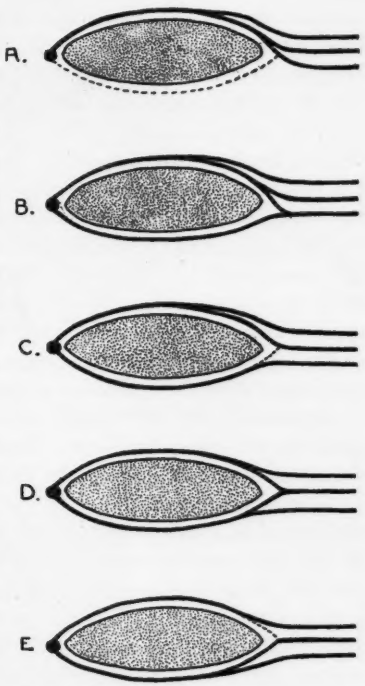

Fig. 2. The varieties of the rectus sheath.

The differences in the construction of the sheath are therefore only differences in the relationship of the rectus to the differentiated parts of the deeper of the two primary muscle layers of the lateral trunk; and if each of the secondary layers (obliquus internus and transversus) of the primary deep layer be divided into two further layers, it is possible, by postulating the absence of one of the final layers, to describe the differences in the formation of the sheath on a purely morphological basis (Fig. 2).

It is obvious that such a basis of explanation is entirely artificial, and it must therefore be recognized that here also, as in other regions of the body, the particular relations of muscles are determined not by their homology but by their action. The form of the sheath of the rectus is then the expression of the action of the lateral strata.

The general morphological facts seem to be clear. The differentiation of the lateral abdominal muscle into strata has been determined, at least in part,

by the rhythmical movements of pulmonary respiration. Phylogenetically there are two primary strata, the internal oblique stratum which is differentiated first and the external oblique stratum which is differentiated later; both strata are (in Urodela) in primary union with the ventral rectus. The secondary and definitive muscles arise from the lamination of the primary strata, there being so added the transversus and subvertebralis (from the internal oblique stratum), the obliquus externus superficialis (from the external oblique stratum), and the rectus superficialis from the ventral rectus. In their further history there is undoubtedly an unequal development of the secondary strata and even some retrogression of some of them (in Anura of the primary internal oblique); so that there are, as a rule, in reptiles, birds, and mammals three lateral muscles. The orthodox view is that the mammalian muscles are the obliquus externus superficialis (the deep externus having undergone retrogression in the abdominal wall though it persists in the thoracic wall), the obliquus internus, and the transversus; and the mammalian rectus is the rectus profundus, the pyramidalis possibly being a part of the rectus superficialis. This arrangement of laminae would explain satisfactorily the anterior position and the independence of insertion of the aponeurosis of the external oblique in the linea alba in the sub-umbilical region in the human subject (in Insectivora the aponeurosis has an independent insertion in its whole length), and allow it to be assumed that, strictly speaking, the external oblique aponeurosis is not a true part of the rectus sheath but a superficial covering of it. The fibres of the external oblique aponeurosis, it may be stated, do not fuse or form any connexion with the tendinous intersections of the rectus but pass freely over them as a complete layer, and at these places the external and internal oblique aponeurotic systems are easily separated. The first intersection in the rectus occurs at the level of the upper margin of the internal oblique.

It is now generally held that in mammals the musculature of the ventral abdominal wall arises not in a prolongation of the myotomic mesoderm but directly in mesenchyme, which may or may not be derived from the myotomes; and that in its development, therefore, this musculature resembles the musculature of the head, the tongue, and the limbs. The developmental history of the ventro-lateral muscle in the human subject shows the rectus to be the ventral part of the internal oblique stratum. In the 20 mm. embryo (Fig. 3) the three lateral strata and the rectus anlage are defined. The superficial and deep strata are continued ventrally, independently of the rectus mass, towards the umbilical margin. The rectus mass is as yet not differentiated, but the central area of it is obviously pre-muscle tissue while the peripheral area is the muscle sheath. The amount of the muscle sheath is considerable and, as is to be seen in the 60 mm. embryo (Fig. 4), there are formed from it the dense fibrous bands at the margins of the rectus[1] and the looser ventral and dorsal walls of the sheath proper. The earlier purely bursal condition of the sheath,

[1] These marginal bands are fully described by Eisler; in the adult they are attached to the medial and lateral margins of the rectus and the angles of the sheath, and, with the rectus, subdivide the cavity of the sheath into anterior and posterior compartments.

however, has been altered in the later embryo by the attachment to it of the aponeurosis of the internal oblique, and through the sheath the internal oblique muscle now reaches its insertion in the linea alba. The ventral and dorsal

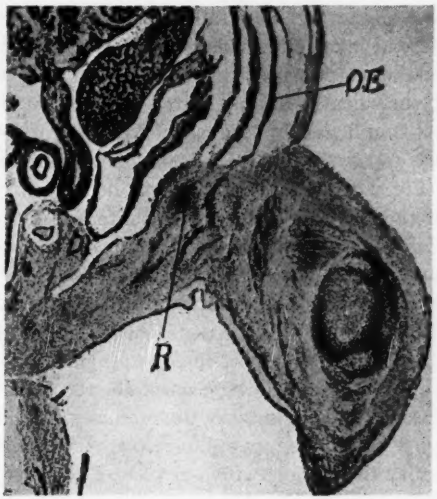

Fig. 3. Transverse section of the abdominal wall of a 20 mm. human embryo.[1]

walls of the sheath thus become aponeurotic, and as such are expressions of the function and manner of action of the internal oblique; and the external oblique and transversus aponeuroses maintain their primary superficial and

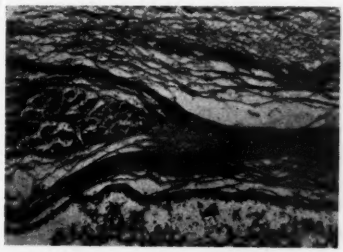

Fig. 4. Transverse section of the abdominal wall of a 60 mm. human embryo.

deep relations to the sheath and are separate from it (Fig. 4). In those forms in which in the adult the internal oblique aponeurosis passes either wholly into one wall or in unequal amounts into the dorsal and ventral walls of the sheath, it must be assumed that the plane of the action of the muscle is not in

[1] Portion of figure from the "Development of the ventral abdominal walls in man", F. P. Mall (1898), *J. Morph.* vol. XIV, p. 347.

the coronal plane through the rectus mass but in a plane partly or wholly on one or other side of it. In the latter condition, for example in the baboon where the internal oblique "aponeurosis" passes wholly in front of the rectus, I have been able to demonstrate the posterior wall of the true rectus sheath between the rectus muscle and the transversus aponeurosis; it is a distinct non-aponeurotic fascial layer and when traced laterally becomes continuous with the internal oblique aponeurosis. In the human subject also the proper posterior wall of the sheath is represented below the arcuate line (linea semicircularis) by a thin delicate fascial sheet which is distinct from the fascia transversalis. The comparative differences in the form of the typical parts of the rectus sheath (Fig. 2 *c*, *d*, and *e*) can be explained then in this way, namely, by the relation of the plane of action of the internal oblique to the rectus. The sheath proper itself is primarily a true rectus sheath and is derived from the rectus mass, but it gains its final significance only when it is considered in mechanical terms of the muscle resultants of the lateral muscles; the sheaths of the two sides then become equivalent, as has been pointed out by Solger (1886 *et seq.*), to the central tendon of the diaphragm.

The atypical condition of the lower part of the rectus sheath occurs in the lowest of the three regions of the anterior abdominal wall, that is, in the human subject, in the region below the interspinous line. It is well known that in its developmental history this region, which in the early foetus is relatively much smaller than in the newborn, differs from the upper regions of the abdominal wall in its much later muscularization; and most of the explanations of the atypical sheath are based on this fact. A final statement of the developmental history of the musculature of this region and of the causes of its late appearance has, I believe, not yet been given. It is a striking fact that even in Teleostei the posterior part of the rectus system develops differently from the anterior part, in that its segmentation occurs after it has lost all connexion with the myotomes (Harrison, 1894); that the segmentation does occur indicates that in teleosts there are mechanical causes which favour segmentation. It is probably true that there is some causal relation of the lateness of the muscularization to the temporary extra-abdominal position of the intestines, to the developmental relations of the urachus, to the course of the intra-abdominal parts of the umbilical arteries, to the development of the processus vaginalis, and to the flexed-adducted position of the lower limbs and their contact with this region of the abdominal wall. That these factors are the causes of the atypical form of the rectus sheath, however, as is advanced in the explanations of Henle, Gegenbaur, Douglas, and Eisler,[1] cannot be maintained, for in

[1] The explanations of the atypical sheath, all of which have been shown to be not correct in fact, are as follows: Henle—to allow the passage of the inferior epigastric artery within the rectus sheath; the artery perforates the sheath far below the arcuate line. Gegenbaur—due to the contact of the embryonic bladder with the abdominal wall and its recession later in development; the bladder never reaches the arcuate line. Douglas—due to the course of the umbilical arteries. Eisler—due to the development of the processus vaginalis; the possibility of the processus is due to the nature of the wall.

many forms, the chimpanzee for example, the lower part of the sheath is not atypical from the parts above, that is, in the chimpanzee the transversus muscle is not displaced forwards and there is therefore no arcuate line.

I am as yet unable to explain the retention of the typical form of the lower sheath in the chimpanzee, but the atypical form in the human subject is due, I believe, to a difference in the function of the lowest part of the abdominal wall; and this view is supported, I consider, by the structural arrangements which I have summarized below:

(1) The arcuate line lies in the early foetus immediately distal to the umbilicus. It migrates distally as the infra-abdominal muscles develop and, generally speaking (i.e., in not less than 70 per cent of adult subjects, Chouke, 1935), it lies on the interspinous line. The fold may fail to descend to its normal position but then, as when it is in the normal position, its medial part is formed by the fibres of the transversus and its lateral part by the fibres of the internal oblique which arise from the anterior end of the crest of the ilium; the fold represents, therefore, the lower edge of the parts of the muscles which have a fixed bony origin from the iliac crest.

(2) Distal to the arcuate line the deep wall of the rectus sheath is formed by a thin fascial layer which is easily separated from the fascia transversalis. As has frequently been described (Mackay, 1889) there is a very constant arrangement of fibres in it, and these fibres when they are well developed form the secondary arcuate line (Henle's band) between the true fold and the pubis, and below it the ligament of Hesselbach which extends downwards to the medial part of the inguinal ligament (Braune, 1884). These bands, I have satisfied myself, are always distinct from the conjoined tendon when it is present, though the ligament of Hesselbach may fuse with it; they belong also to the parts of the internal oblique and transversus which arise from the iliac crest, and they represent, as I understand them, the incomplete translation forwards of the aponeuroses into the anterior wall of the sheath and they illustrate transitional stages of the formation of the conjoined tendon.

(3) The lowest intersection of the rectus muscle lies at the level of the interspinous line, that is, at the level of the arcuate line. I found this also to occur in the baboon and a rhesus monkey. The supra-umbilical segments of the rectus as judged by their nerve supply are derived from, or at least are equivalent to, the 7th, 8th, and 9th thoracic myotomes, and the infra-umbilical segments correspond with the 10th, 11th, and 12th myotomes. The segmentation of the rectus, however accurately it may finally correspond to the original segmentation of the 7th to the 12th thoracic myotomes, is generally accepted to be a secondary occurrence, for in the early stages of development (11 mm. embryo, Lewis, 1910) the rectus mass is a continuous sheet in which there are no myosepta. The causes of the segmentation (see Strasser, 1918), whatever they may finally prove to be, operate then as far as the interspinous line and are inoperative below it, so that at least the 11th and 12th myotomes are not separated. The lowest part of the rectus appears therefore to be subjected to

mechanical requirements which are different from those of the upper part, whether these requirements be confined to itself or imposed on it by the lateral muscles.

(4) The lower border of the fleshy belly of the external oblique lies along the interspinous line, the "Muskelecke" of Gaupp (the angular projection between the anterior and lower borders of the fleshy belly) being in my examinations remarkably constantly opposite the anterior superior spine. Thus below the interspinous line the external oblique is entirely aponeurotic; it cannot by itself alter the curvature of this part of the abdominal wall.

The coincidence of these structural changes at the upper level of the hypogastrium strongly suggests a difference in function of the musculature of the upper and lower parts of the anterior abdominal wall; and this difference may be (*a*) in the active and postural contraction of the muscles to produce movement of the trunk, or (*b*) in their passive contraction and relaxation in reciprocal activity with the diaphragm and thoracic wall in respiration, or (*c*) in producing and maintaining a proper intra-abdominal pressure by their tonic activity and so acting as a weight-bearing mechanism for the viscera, or (*d*) in raising the intra-abdominal pressure by active contraction as is required in expulsive acts (and as occurs when the trunk is fixed to act as a basis for the doing of heavy muscular work by the limbs). The analyses of the muscles in these regards are as follows:

1 (*a*). The rectus and in man the external oblique, through their attachments to the thorax above and the pelvis below, are concerned in the maintenance of the posture and in the movements of the trunk, the rectus being more active in the antero-posterior movements and the oblique in the lateral movements. The hypogastric region, since it is between the iliac bones and in this sense part of the pelvis and moving with it, does not take part in these movements; nor is it in man greatly influenced by the movements of the lower limbs. All the flexion lines of the trunk therefore lie above it and the flexion lines of the lower limbs below it. The external oblique over this area is thus free to become aponeurotic in character and, so far as movements of the trunk are concerned, skeletal in function (the inguinal ligament, the epipubic bone). This "skeletal" part of the aponeurosis normally lies on a flattened rather than on a curved plane, is anterior to the rectus, and reaches the linea alba independently, or almost so, of the rectus sheath (Fig. 5). It is in this "skeletal" area that the rectus is unsegmented and unattached to its sheath; and it is here also that it so frequently acquires an attachment to the linea alba. (*b*) The rectus and the external oblique also act as part of the mechanism for the weight carrying of the viscera, transferring the weight to the thorax through their upper attachments. The high extension of both muscles on the thoracic wall which is characteristic of so many forms is to be ascribed to their two functions. In the human subject they extend farther forwards in the female than in the male, as would be expected on this interpretation, which seems to me a better explanation than that "the muscles have regressed less in the female than the

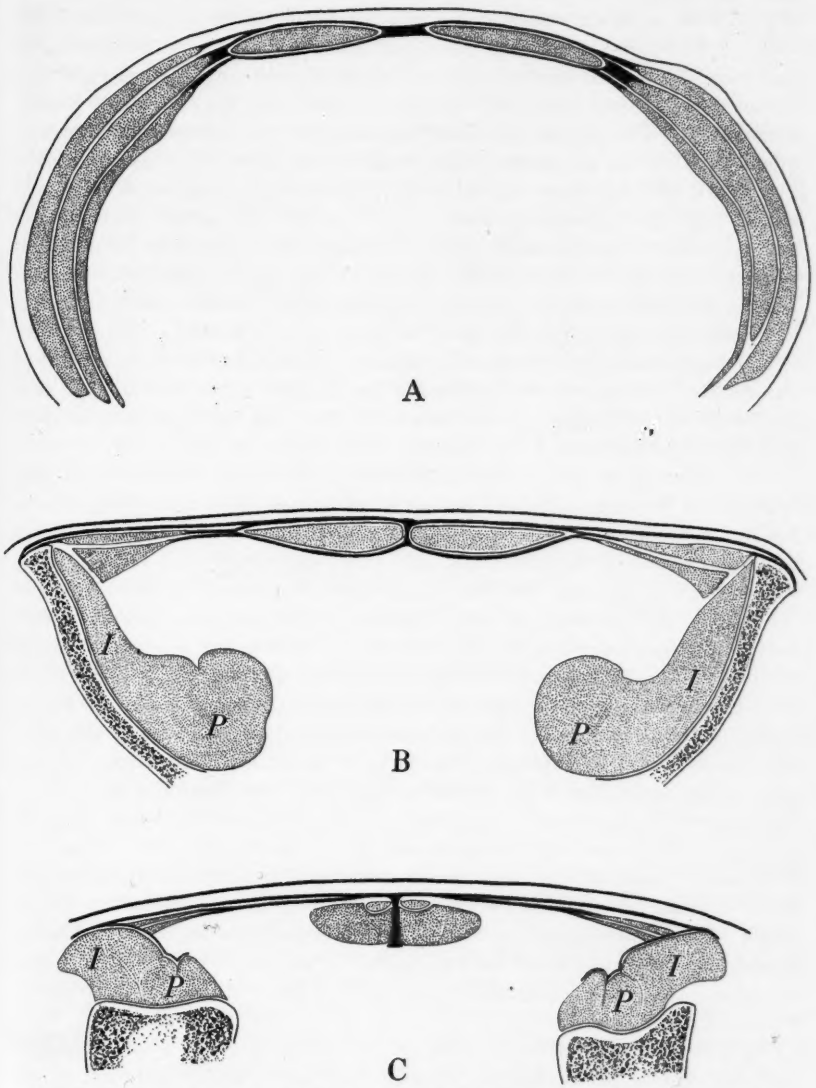

Fig. 5. Transverse sections of an adult male trunk: A, 1 in. above the umbilicus; B, 1 in. below the umbilicus; and C, 1 in. above the symphysis pubis.

male" (Loth, 1931). It is also a striking fact that in older men, when the thoracic curve of the vertebral column is increased and the thorax is ante-flexed, the yielding of the abdominal wall is in what I have termed the "skeletal" area and there are formed there the lateral swellings in the inguinal triangles and the median swelling above the symphysis pubis (the *fleur de lys* of French surgeons). (*c*) The two muscles must also take part in the passive respiratory movements of the abdominal wall. I have been unable to discover in the living subject a difference in kind in the respiratory movements of the upper and hypogastric parts of the wall, apart from the side to side increase and decrease which occurs above but not below; the hypogastric area moves forwards and backwards with the upper areas, though to a much less extent. The backward movement must be produced by the rectus, which when it contracts and diminishes the front to back measurement of the abdomen in the middle line might be expected to cause a counter forward movement in the inguinal triangle. In my experience this does not occur; not does it occur in the active contraction of the rectus with the other abdominal muscles in powerful expulsive acts or the fixation of the trunk for heavy work.

2(*a*) The upper part of the internal oblique, arising from the vertebral column and the iliac crest and lying in the same plane as the rectus (Fig. 5), acts equally well whether it reaches the linea alba in front of or behind the rectus in all movements of the abdominal wall which are purely respiratory, that is, when all the muscles of the abdominal wall act together in relaxation and contraction and the curvature of a horizontal section is increased and decreased both antero-posteriorly and from side to side. When the upper part of the internal oblique acts with the rectus and external oblique, however, especially with those of the opposite side, to flex the costal margin towards the pelvis, a position in front of the rectus is mechanically better, but when it acts with the transversus as an expulsive constrictor of the abdomen it is better placed deep to the rectus. The active function must be the chief function in the many forms, for example, the baboon and the chimpanzee, in which it passes wholly in front of the rectus. (*b*) The upper part of the transversus obviously acts as a circular compressor of the thoracic outlet and the abdominal cavity; its fibres can take no primary part in the postural or active movements of the trunk. Its morphological position deep to the rectus is its best mechanical position and its origin from the deep surface of the thoracic wall ensures that it will maintain it; in comparative anatomy its position deep to the rectus is constant.

3. The lower parts of the internal oblique and transversus, attached as they are wholly to the pelvis and the "skeletal" area of the abdominal wall, cannot be concerned in the postural position or the movements of the trunk. Their activity must be localized within the area in which they lie. It is unnecessary, I think, to postulate a highly specialized action for them, as, for example, that they are sphincter mechanisms for the deep abdominal ring. They are part of the expulsive musculature, they contract with it, and they prevent the forward

movement of the "skeletal" area of the hypogastrium which would otherwise occur when the upper parts of the abdominal muscles contract. In this sense they are antagonists to them, and especially to the lower part of the rectus, rather than active agents in raising the intra-abdominal pressure; and in this interpretation the eruption of the testis below their lower border is more easily understood, and, in their relatively slight strength or defective development, the genesis of inguinal hernia is better appreciated. It appears to me that they may act in the same way as reciprocal muscles to the iliacus and psoas which, lying close behind them (Fig. 5), will alter the pressure in the hypogastric abdomen when they contract. If this difference in the action of the upper and lower parts of the internal oblique and transversus muscles is accepted, it becomes possible to explain the interval which sometimes is found between them, the possibility of a difference in their ventral extension, and the sharp definition of the arcuate line. The upper parts of the muscles are active energetic contracting parts, while the lower parts, much less active and containing much less contractile substance, only resist the downward pressure of the diaphragm and of the upper parts of the abdominal wall. The arcuate line is the lower edge of the upper parts.

The anterior position of the aponeuroses of the lower parts of the internal oblique and transversus is the most favourable which is possible for this "resisting" action, for their fibres then act on the most curved surface which is available; they also then pass over the rigid pillar which the contracted rectus forms for them. The anterior position is thus due to more than simply the shifting forwards and more anterior position of their origin, for the muscle fibres which are attached to anterior aponeuroses will in virtue of their greater curvature contract earlier and remain contracted longer than fibres which are attached to posterior aponeuroses, and, as it were, they will develop at their expense. The sheath of the rectus even in its variations thus remains the expression of the action of the lateral muscles.

SUMMARY

1. Developmentally the sheath is a true rectus sheath derived from the rectus mass, but as the lateral muscles obtain attachment to it, it assumes an aponeurotic character.

2. The sheath gains its final significance only when it is considered in mechanical terms of the muscle resultants of the lateral muscles.

3. The typical portion of the rectus sheath exists in three main forms, each form being an expression of the action of the lateral abdominal muscles.

4. The atypical form of the lower part of the rectus sheath is due to a difference in the function of the lower parts of the abdominal muscles.

5. The arcuate line (linea semicircularis) is the lower edge of the upper actively contracting parts of the abdominal muscles.

6. The sheath of the rectus, even in its variations, remains the expression of the action of the lateral muscles.

In conclusion, I should like to acknowledge the help and guidance of Prof. J. C. Brash in the preparation of this paper, and to thank Mr J. Borthwick of this Department for the photographs.

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ANATOMICAL NOTES

A FURTHER EXAMPLE OF CERVICAL INTERCOSTAL ARTICULATION

By A. J. E. CAVE
Royal College of Surgeons of England

In this *Journal* some time ago (1934) I drew attention to a distinctive but remarkably rare manifestation of irregular vertebral segmentation affecting the cervical spine, viz. the occurrence of adventitious diarthrodial union between the pleurapophyseal elements of two adjacent cervical vertebrae. I described a particular example, involving the left sides of the third and fourth vertebrae, and made reference to one previous case in the literature, that noted by Grunbaum (1891), wherein the left sides of the sixth and seventh cervical vertebrae were involved. By an oversight reference was omitted to a still earlier case described by Bianchi (1889), that of a left-sided intercostal articulation between the sixth and seventh cervical vertebrae in a woman of thirty years.

My former communication induced Dr T. D. Stewart (1934) to place on record an example from a spine in the U.S. National Museum—that of an adult male North American Indian, from a prehistoric site in Kentucky, manifesting a right-sided adventitious diarthrosis between the costal elements of the fifth and sixth cervical vertebrae.

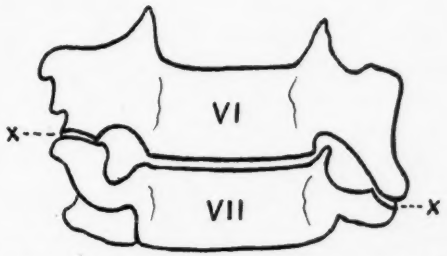

Fig. 1. Sixth and seventh cervical vertebrae showing bilateral asymmetrical adventitious articulation (x, x).

To these four recorded cases must now be added the present, and even more interesting specimen, for the details of which I am indebted to Dr Stewart.

This new example was encountered in the spine of an adult female Florida Indian, exhibiting concomitant errors of vertebral segmentation. A bilateral intercostal diarthrodial articulation occurs between the sixth and seventh cervical vertebrae. The precise mode of adventitious articulations differs on the two sides, on the right resembling that described by Stewart (1934) in his Amerindian male, and on the left resembling that obtaining in my European specimen. The asymmetry of these additional joints is shown in the text-figure.

In this same Florida spine the atlas vertebra is deficient both mid-ventrally and mid-dorsally (a rare combination) and its right lateral mass is continuous with the corresponding occipital condyle. There is fusion of the axis with the third vertebra,

and of the fifth with the sixth vertebra. The fourth and fifth cervicals lack the right moieties of their neural arches, whilst the second of the thirteen thoracic vertebrae present manifests spina bifida. Defective segmentation has therefore affected this column both numerically and structurally.

The interest of this case is twofold. It constitutes the first recorded example of bilateral cervical intercostal articulation, whilst the association of this condition with other, more emphatic and better-known vertebral errors of segmentation, substantiates the view previously expressed as to its true nature, viz. that cervical intercostal articulation is a genuine vertebral variation and no merely fortuitous or bizarre configuration of parts.

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ABNORMAL BIFURCATION OF AORTA

By G. I. BOYD
Leeds

THE somewhat rare condition here described was discovered during dissection of an adult male body which presented no other abnormality beyond an atrophied right kidney and thickened ureter.

The aorta bifurcated at the level of the third lumbar vertebra, the right common iliac artery passing to the right under cover of the inferior vena cava, and the left

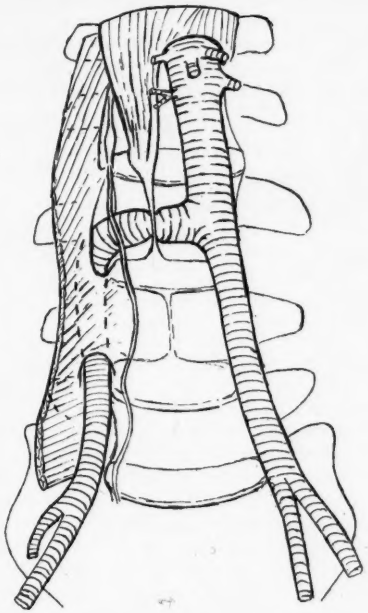

Fig. 1.

Fig. 2.

Fig. 1. Lumbar vertebrae and aorta from the front. Crura of diaphragm, medial edge of right psoas and right sympathetic trunk have been preserved *in situ*.

Fig. 2. Right side of specimen in Fig. 1.

common iliac artery being the continuation of the aorta. The right common iliac artery was constricted by a fibrous slip from the right crus of the diaphragm which passed down in front of it to the discs between the third, fourth and fifth lumbar vertebrae (see Fig. 1). It was then crossed by the right lumbar sympathetic trunk and passed downwards and backwards into the psoas muscle which formed a tendinous arch over it. The abnormal common iliac artery emerged from the psoas through

another tendinous arch opposite the disc between the fourth and fifth lumbar vertebrae and ran down on the right side of the commencement of the inferior vena cava.

While under cover of the psoas muscle the right common iliac artery gave origin to the third and fourth right lumbar arteries, and to a branch which descended over the fifth lumbar vertebra to the ala of the sacrum (see Fig. 2). The third and fourth left lumbar arteries arose from the back of the continuation of the aorta.

Discussion

The relationship of the abnormal common iliac artery to neighbouring structures suggests that it has originated in the enlargement of the third right lumbar artery, and has then followed the course of an intersegmental anastomosis as far as its usual point of bifurcation into external and internal iliac arteries. It is noteworthy that in spite of the constrictions of the artery produced first by the downward prolongation of the right crus and then by the passage of the artery through the psoas both lower limbs were equally developed.

Quain (1) notes the constancy of the point of bifurcation of the aorta, and quotes an instance of bifurcation immediately below the origin of the right renal artery recorded by Haller; and division opposite the second lumbar vertebra observed by Boinet, Cruveilhier, and Eckhard.

REFERENCE

(1) Quain (1892). *Anatomy*, 10th ed., vol. II, part II, p. 458.

A RELATION OF THE SCIATIC NERVE

By A. R. PARKES, *Department of Anatomy, Bristol University*

Our attention was first directed to the subject of this note by Prof. Rendle Short of Bristol who has already dealt with its possible surgical importance in a paper(1) in the presentation of which we of the above Department took part. In this paper Prof. Rendle Short describes how he found a firm crescentic fibrous band pressing on the antero-lateral border of the sciatic nerve in the region of the greater sciatic foramen, and it is with the situation and connexions of this band that I wish to deal.

Dr Llewelyn and I examined a number of cadavers and in one or two cases a definite band was felt by the exploring finger in the position described by Prof. Rendle Short. We were, however, unsuccessful in our early attempts to display the band, for, when the piriformis muscle was cut and turned back, the band seemed to lose its identity, the reason for which will soon be made clear. Recently we have, by more careful raising of the piriformis muscle, been able to display the band in varying degrees of development in several subjects and to study its anatomical connexions.

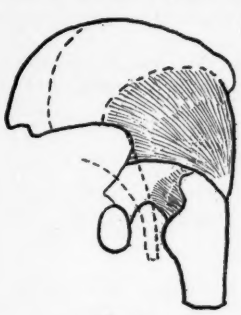

Fig. 1.

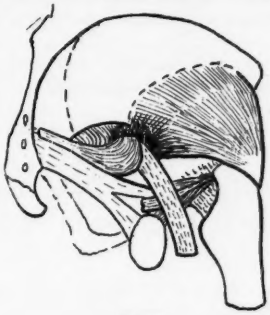

Fig. 2.

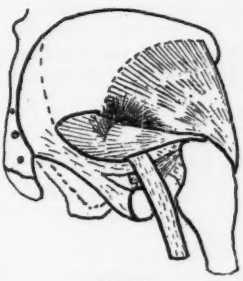

Fig. 3.

The first point I would emphasize is that in many cases—and certainly in those in which we found the band well developed—the lower and hinder part of the origin of gluteus minimus extends very much further down along the anterior border of the greater sciatic notch than is usually depicted in the textbooks—so much so that the antero-lateral part of the sciatic nerve, after emerging from the foramen, lies on this part of the muscle (Fig. 1). Secondly, the fascia covering the gluteus minimus muscle extends backwards to become continuous with the fascia covering the proximal part of the superficial surface of the piriformis muscle. Now the firm crescentic band referred to above appears to be a thickening of this fascia and extends from the lower and hinder part of the gluteus minimus muscle, where it lies deep to the sciatic nerve, upwards and medially in close relationship with the antero-lateral border of the nerve, finally curving back over the upper border of the piriformis on to the superficial surface of that muscle (Figs. 2 and 3).

Connexions—tendinous, muscular, and fascial—between the piriformis and gluteus minimus muscles are of frequent occurrence and their morphological significance has been dealt with by Frazer(2) and others. However, the fact that a fascial band such as that described above can be in intimate relationship with the sciatic nerve and may, therefore, have some surgical importance, has not, so far as I am aware, been pointed out before.

REFERENCES

(1) Short, A. R. (1936). *Bristol Med. Chir. J.* (summer issue).
(2) Frazer, J. E. (1904). *J. Anat. Physiol.* vol. xxxviii, p. 170.

REVIEWS

Traité d'Embryologie des Vertébrés. A. Brachet. Nouvelle Édition revuée et complétée. Par A. Dalcq et P. Gérard. (Paris: Masson et Cie, Éditeurs.) 1935. Pp. viii + 690. Figs. 603. Broché, 110 fr.; cartonné toile, 130 fr.

This very valuable book has lost nothing by passing into the hands of its present authors. They have retained all the originality, the logical clarity, and the style of the book which it received from the personality of the great Brachet.

The present authors have brought the classical conceptions of embryology into harmony with the work of recent years. The earlier chapters on gastrulation, the formation of the embryo, the foetal membranes, and the origin of the gonocytes have been rewritten. Wherever information derived from experimental work and throwing light on the problems of ontogeny has been available the authors have incorporated it in the text.

It is a most excellent book, and teachers and students will probably regard it as the most convenient manual within an assimilable compass upon the subject of comparative embryology.

Symposia on Quantitative Biology. Vol. iii. (New York: The Biological Laboratory, Cold Spring Harbour, Long Island.) 1935. Pp. xv + 359. No price stated.

In an introduction to this volume it is explained that each summer the laboratory invites a group of mathematicians, chemists and biologists—all interested in some specific aspect of quantitative biology—to a discussion which endures for five weeks. The present volume of essays has been compiled from these discussions. The volume contains thirty-five special articles. The articles consist of the contribution made by whoever introduced the subject, and the remarks with names of those who took part in the discussion. It is not possible to give a list of all the titles, but in this volume every conceivable biological aspect of light has been discussed by those who by universal consent are regarded as the masters of the subject.

Physiologie der Inneren Sekretion. By Prof. Dr Leon Asher. (Leipzig: Franz Deuticke.) 1936. Pp. xii + 395, 94 figs. and 2 tables. Price M. 20, geb. M. 23.

This monograph on the ductless glands includes a detailed account of each member of this series, but in reviewing the activities of each the author has endeavoured to bring out the contribution that is made towards the co-ordination and the integration of the organism as a whole. The work is complete, well documented, accurate and forms a monograph which takes its place with others of a similar kind. It affords a ready means to anyone who wants quickly to become conversant with the present state of knowledge in this subject. The dominant position of the hypophysis has been the subject of scientific eloquence for some time. It is refreshing to find in this monograph that it, along with the hypothalamus, forms the title of the last chapter in the book.

RECENT APPOINTMENTS

Dr Frank Goldby appointed Professor of Anatomy in the University of Adelaide.

Dr Donald Sheehan appointed Professor of Anatomy in the College of Medicine, University of New York.

SIXTH MEETING OF THE INSTITUT INTERNATIONAL D'EMBRYOLOGIE[1]

Short communication by the SECRETARY-TREASURER

The International Institute of Embryology, whose object is the advancement of the comparative embryology of Vertebrates by creating scientific and friendly relationships among the principal investigators, by founding a collection of rare embryological material and an international library, held its biennial meeting at Turin on 31 August and 1 September of last year in the Anatomical Institute under the kind hospitality of Prof. G. LEVI.

In spite of the fact that only seven members were able to attend, the meeting was very interesting from a scientific point of view and certainly may be considered to have advanced the purposes of the Institute.

In the private session the proposed changes in the statutes were approved and the original board was re-elected. So its composition remains: J. BOEKE (Utrecht), President; O. GROSSER (Prague), Vice-President; D. DE LANGE (Utrecht), Secretary-Treasurer.

The meeting made the proposal to bestow the honorary membership on six persons: F. HOCHSTETTER (Vienna), THOMAS H. MORGAN (Columbia University, New York), A. NICOLAS (Nancy), F. GRAF VON SPEE (Kiel-Holtenau), J. T. WILSON (Cambridge, England), EDM. B. WILSON (Columbia University, New York); and proposed the election of eight other persons as efficient members: A. J. P. VAN DEN BROEK (Utrecht), Miss H. FELL (Cambridge, England), CARL HARTMAN (Baltimore), J. HOLTFRETER (Munich), N. K. KOLTZOFF (Moscow), WILHELM VON MÖLLENDORF (Zürich), T. TERNI (Padua), G. WISLOCKI (Harvard University, Cambridge, Mass.). These proposals were approved later by the absent members.

Finally Prof. LEVI expressed a wish that the Institute should propose one or two subjects for investigation suitable for the scientific collaboration of the members of the Institute. In the discussion Prof. LEVI proposed as a possible theme: "The influence of the constitution on embryological variations"; while Prof. CELESTINO DA COSTA had a predilection for the following: "A comparative investigation of the first stages of development in Mammals and of the connexions between the phenomena characterizing that period".

Two sessions were devoted to the demonstration of microscopical preparations, films and lantern slides. The programme contained the following subjects:

(1) Young stages of the macaque, Prof. STREETER (Baltimore).

(2) Young stages of *Galago Demidoffi*, Dr GÉRARD (Brussels).

(3) Amniogenesis of the Hedgehog, Prof. CELESTINO DA COSTA (Lisbon).

(4) Development of the paraganglia in Bats, Prof. CELESTINO DA COSTA (Lisbon).

(5) Cinematographic demonstration of tissue-cultures of spinal ganglia of chicken and human embryos, Prof. LEVI (Turin).

(6) Microscopical preparations of fixed tissue-cultures of spinal ganglia and of the spinal medulla, coloured by a slightly modified Cajal-method, Prof. LEVI (Turin).

(7) The bursa ovarii of the Hedgehog showing a well-developed connexion between the rete ovarii and the epithelium of the ostium tubae or of the ovarial sac, Prof. DE LANGE (Utrecht).

(8) Terminal reticulum of the peripheral sympathetic nerve-system in fat-cells, sebaceous glands, blood vessels, and striated muscle fibres, Prof. BOEKE (Utrecht).

The demonstrations were followed by interesting discussions on the interpretation of the observed phenomena. This meeting may be considered a success notwithstanding the fact that only a few members of the society were present.

[1] The address of the association is The Hubrecht-Laboratory, Janskerkhof 2, Utrecht (Holland).

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